New Species, Combinations, and Lectotypifications in Neotropical and Northern Mexican *Frangula* (Rhamnaceae)

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Abstract. In preparing the family Rhamnaceae for an upcoming volume of *Flora Mesoamericana*, it became apparent, based on recent molecular work (Bolmgren & Oxelman, 2004; Bolmgren, pers. comm., 2013), as well as historical (Grubov, 1949; Kartesz & Gandhi, 1994), and personal morphological studies, that recognization of the genus *Frangula* Mill. is well supported. The emphasis of the current study has been on Mesoamerican species and four species from Mesoamerica, *F. circumscissa* A. Pool from Costa Rica, *F. darienensis* A. Pool from Panama, *F. grandiflora* A. Pool described from Honduras and also found in Chiapas, Mexico, *F. pendula* A. Pool described from Costa Rica and also found in Panama, and one species from Oaxaca, Mexico, *F. inconspicua* A. Pool, are published here as new. Four Mesoamerican species and two varieties published in *Rhamnus* L. are transferred to *Frangula* as: *F. breedlovei* (L. A. Johnst. & M. C. Johnst.) A. Pool [≡ *R. breedlovei* L. A. Johnst. & M. C. Johnst.], *F. mcvaughii* (L. A. Johnst. & M. C. Johnst.) A. Pool [≡ *R. mcvaughii* L. A. Johnst. & M. C. Johnst.], *F. oreodendron* (L. O. Williams) A. Pool [≡ *R. oreodendron* L. O. Williams], *F. wendtii* (Ishiki) A. Pool [≡ *R. wendtii* Ishiki], *F. capreifolia* var. *grandifolia* (M. C. Johnst. & L. A. Johnst.) A. Pool [≡ *R. capreifolia* var. *grandifolia* M. C. Johnst. & L. A. Johnst.], and *F. discolor* var. *mesoamericana* (L. A. Johnst. & M. C. Johnst.) A. Pool [≡ *R. sphaerosperma* var. *mesoamericana* L. A. Johnst. & M. C. Johnst.]. The following new combinations are made for five Mexican species north of the Flora Mesoamericana area: *F. chimalapensis* (R. Fernández) A. Pool [≡ *R. chimalapensis* R. Fernández], *F. hintonii* (M. C. Johnst. & L. A. Johnst.) A. Pool [≡ *R. hintonii* M. C. Johnst. & L. A. Johnst.], *F. longistyla* (C. B. Wolf) A. Pool [≡ *R. longistyla* C. B. Wolf], *F. scopulorum* (M. E. Jones) A. Pool [≡ *R. serrata* var. *scopulorum* M. E. Jones], and *F. surotatensis* (Gentry) A. Pool [≡ *R. surotatensis* Gentry]. Four South American species are transferred: *F. acuminata* (Maguire & Steyerm.) A. Pool [≡ *R. acuminata* Maguire & Steyerm.], *F. chimantensis* (Steyerm. & Maguire) A. Pool [≡ *R. chimantensis* Steyerm. & Maguire], *F. marahuacensis* (Steyerm. & Maguire) A. Pool [≡ *R. marahuacensis* Steyerm. & Maguire], *F. neblinensis* (Maguire & Steyerm.) A. Pool [≡ *R. neblinensis* Maguire & Steyerm.]. *Rhamnus sphaerosperma* var. *longipes* M. C. Johnst. & L. A. Johnst. (from Hispaniola and Puerto Rico) is transferred to *Frangula* and raised to the rank of species, necessitating the publication of the new name *F. longipedicellata* A. Pool. Lectotypes are designated for *F. polymorpha* Reissek, *R. citrifolia* Rusby, and *R. riojae* Perkins.

Key words: Frangula, IUCN Red List, Mesoamerica, Mexico, Rhamnaceae, *Rhamnus*, South America, West Indies.

The genus *Frangula* Mill. (Rhamnaceae) consists of approximately 50 species and is native to North America, the Neotropics, Europe, and Asia. Grubov (1949) published a worldwide revision of *Rhamnus* L. s.l. and provided names in *Frangula* for those species known to him. His generic recognition of *Frangula* was accepted in Europe for the Flora Europaea (Tutin, 1968) and for taxonomic treatments in North America (Kartesz & Gandhi, 1994; G. Nesom, Flora of North America, in prep.). However, most modern Neotropical works (e.g., Standley & Steyermark, 1949; Nowicke, 1971; Johnston & Johnston, 1978; Fernández N., 1986; Johnston, 2001; Steyermark & Berry, 2004) have continued to treat the species of *Frangula* in *Rhamnus*. Johnston and Johnston (1978), who recognized *Frangula* at the subgenus level within *Rhamnus*, provided a translation of the characters used by Grubov (1949 [Russian]) to distinguish *Frangula* from *Rhamnus*, and Kartesz and Gandhi (1994) provided a similar table of distinguishing characteristics, which is slightly revised here (Table 1). The most convincing characteristics for recognizing *Frangula* include the bud scales absent, the pyrenes (Fig. 1A) indehiscent, and the seeds smooth with a thickened cartilaginous basal rostrum that is exserted through the base of the pyrene. In contrast, in *Rhamnus*, the bud scales are present, the pyrenes (Fig. 1B) ventrally dehiscent, and the seeds (Fig. 1C) grooved, without a basal thickening and completely enclosed within the

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Table 1. Comparison of *Frangula* Miller with *Rhamnus* L.

	Frangula	*Rhamnus*
Bud scales	absent	present
Thorns	absent	present or absent
Leaves	alternate (rarely some opposite)	alternate or opposite (or both)
Flowers	bisexual, usually 5-merous (rarely 4-merous)	unisexual or bisexual, 4- or 5-merous, usually unisexual and 4-merous
Hypanthium	circumscissile far below sepal bases (rarely not circumscissile)	not circumscissile (rarely circumscissile at or just below sepal bases)
Sepals	fleshy with keel apparent	usually chartaceous with inconspicuous keel
Petals	well-developed, basally clawed	poorly developed, without claw, or sometimes absent in pistillate flowers
Ovary	usually 3-locular (rarely 2)	2- to 4-locular
Style/Stigma	style simple, usually included, with trifid stigma	style 2 to 4 deeply cleft, usually exserted, each with simple stigma
Pyrenes	indehiscent, open at base	dehiscent, closed at base before dehiscence
Seeds	without groove, with thickened basal rostrum exserted through base of pyrene	with groove, without thickened rostrum, totally contained in pyrene before dehiscence

pyrene before dehiscence. The species treated in this paper as *Frangula* are consistent with these characteristics. They also share the other characteristics of *Frangula* in being unarmed and having alternate leaves (leaves both alternate and opposite in *F. granulosa* [Ruiz & Pav.] Grubov), the flowers always bisexual (Fig. 1J–L), 5-merous with the hypanthium usually circumscissile (rarely not, cf. discussion for *F. breedlovei* (L. A. Johnst. & M. C. Johnst.) A. Pool), the sepals fleshy and distinctly adaxially keeled, the petals well developed with limb and claw, the style simple with a 3-lobed stigma (usually briefly so) that is usually included (sometimes equaling sepals, as in *F. longistyla* (C. B. Wolf) A. Pool), and the ovary 3-locular with three pyrenes usually developing. In contrast, *Rhamnus* often has branch tip thorns, alternate or opposite leaves, predominately unisexual flowers (Fig. 1D–I) that are 4- or 5-merous (usually 4-merous) with the hypanthium not circumscissile (rarely circumscissile at, or slightly below, the base of the sepals), the sepals chartaceous and inconspicuously keeled, the pistillate flowers often without petals or petals greatly reduced without a basal claw, the style usually deeply 2- to 4-parted and exserted, and the ovary 2- to 4-locular, with two to four pyrenes developing.

The molecular study of Bolmgren and Oxelman (2004) included 22 species of *Rhamnus* s.l., the seven species of *Frangula* from Europe, China, U.S.A., Mexico, and Brazil and from the three informal (i.e., not validly published) sections recognized by Grubov. While not answering all the possible generic questions in *Rhamnus*, this analysis was based on both chloroplast and nuclear sequence, *trnL-F* and ITS, respectively. Results found *Frangula* to be "a well supported monophyletic sister clade to the rest of *Rhamnus* in its widest sense" (Bolmgren & Oxelman, 2004: 386). This was a strong statement, supporting the recognition of *Frangula* at the genus level. A further, unpublished molecular study, including 25 species of *Rhamnus* s.l. (16 in *Frangula*, including *F. granulosa*, unusual in this genus in having the hypanthium not circumscissile and the leaves both alternate and opposite), further supports this conclusion (Bolmgren, 2013, pers. comm.).

The current study, while emphasizing the Mesoamerican species, provides names in *Frangula* for all species in the Western Hemisphere, for which the types have been examined and that can be confirmed as independent species, in need of recognition. There are ca. 44 species of *Frangula* in the Western Hemisphere with ca. 37 species from Mexico and the Neotropics. The 19 species names and two variety names published here add to the names previously published in *Frangula*, for Mexico and the Neotropics, by Reissek (1861), Grubov (1949), and Kartesz and Gandhi (1994). Remaining in *Rhamnus* s. str., for the Western Hemisphere, are ca. 18 species, with only one, *R. serrata* Schult., found in the Neotropics (Mexico and Guatemala). While previous studies of *Rhamnus* s.l. have relied on leaf characteristics (e.g., Standley & Steyermark, 1949; Johnston & Johnston, 1978; Johnston, 2001; Steyermark & Berry, 2004), a number of other characteristics are relevant to the distinction of the taxa, namely the persistence of stipules, inflorescence characteristics such as the pedicel length relative to the subtending petiole length, and sessile or pedunculate inflorescences (but both in a few species, such as *F. capreifolia* (Schltdl.) Grubov, *F. discolor* (Donn. Sm.) Grubov, and *F. marahuacensis* (Steyerm. & Maguire) A. Pool). Useful floral characteristics, in particular, include the hypanthium shape and whether the hypanthium is

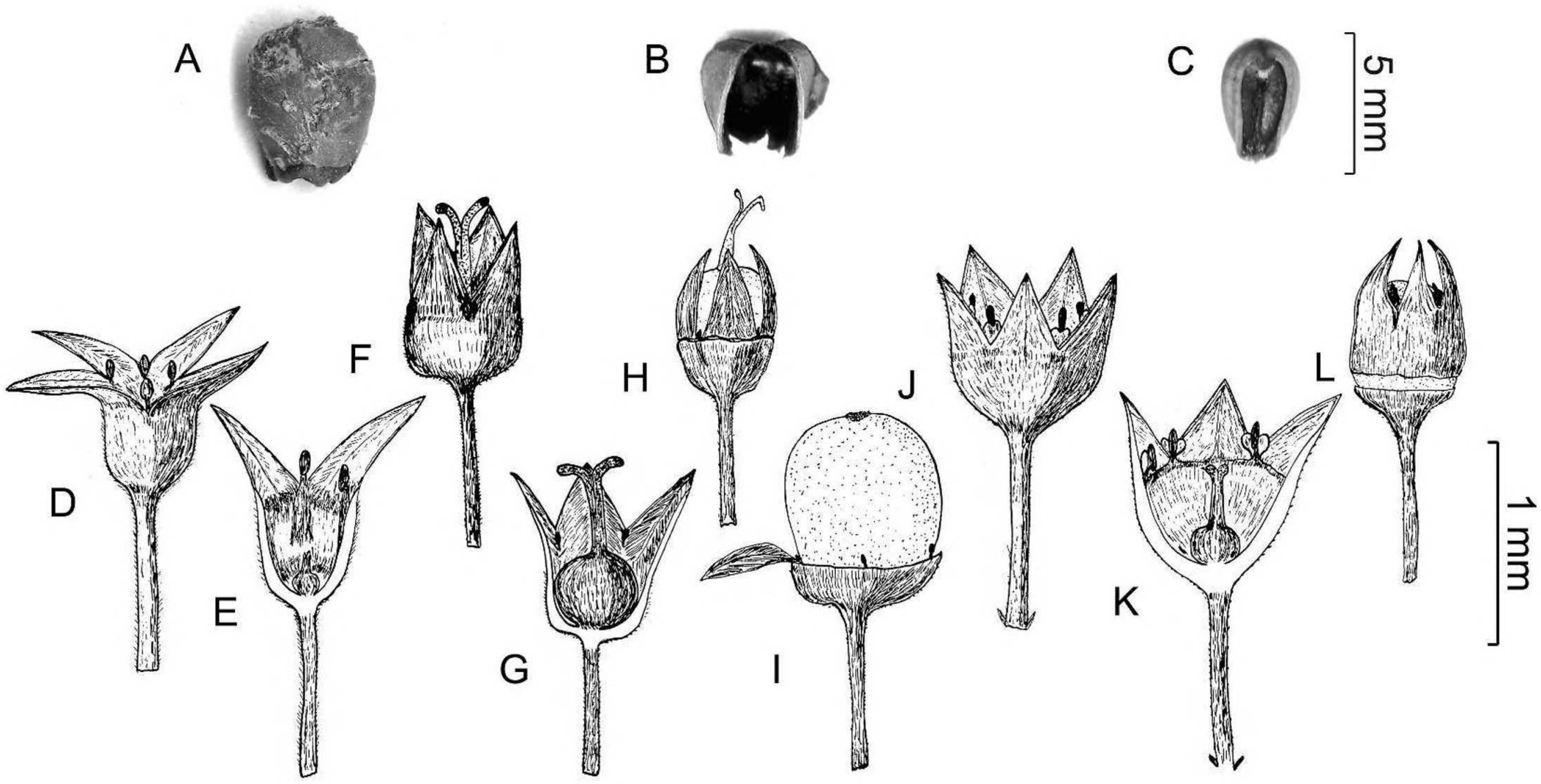

Figure 1. —A. *Frangula discolor* (Donn. Sm.) Grubov var. *discolor*. Young indehiscent pyrene with seeds exserted at base. Taken from *S. Lobo et al. 1075* (MO). B, C. *Rhamnus insula* Kellogg. —B. Dehiscent pyrene. —C. Grooved seed. B and C both from *E. Palmer 738* (MO). D–I. *Rhamnus* L. —D, E. Staminate flower, identified in original publication (Wolf, 1938: 8) as "*R. crocea ilicifolia* ♂ fresh material from RSA. Bot. Gard. Prop. No. 183." —F, G. Pistillate flower, in original publication as "*R. crocea ilicifolia* ♀ *C. B. Wolf 4748*" (RSA-6825). —H, I. Young fruit with non-circumscissile hypanthium, in original publication as "*R. crocea ilicifolia*♀ *C. B. Wolf 4630*" (RSA-6961). J–L. *Frangula* Mill. —J, K. Flower. —L. Immature fruit with circumscissile hypanthium. J–L in original publication as "*Rhamnus californica typica* fresh material from RSA. Bot. Gard. Prop. No. 1254"). D–L adapted from Wolf (1938: 8, fig. 1). Reproduced with the permission of the Archives of the Rancho Santa Ana Botanic Garden, Claremont, California, U.S.A.

circumscissile or not, the sepal length relative to hypanthium length, the sepal position as erect, spreading or recurved, and the ovary as glabrous or pubescent.

The conservation status has been estimated for each new taxon, according to IUCN (2012) Red List categories and criteria. However, these preliminary assessments are based only on the estimated extent of occurrence (EOO) and the area of occupancy (AOO), as taken from herbarium specimens, many of which were georeferenced from vague collection localities. Changes in occupancy (Bb, continuing decline, including decline in habitat quality and c, extreme fluctuation), potential threats and area size affected by threats (as criteria for IUCN size of location Ba), population reduction (A), and the number of mature individuals (C, D) are not known for any of the taxa treated here. Nearly all the species treated here are apparently restricted to relatively high elevations and, while most apparently do well in disturbed habitats, they are presumably to some degree subjected to threats.

1. Frangula acuminata (Maguire & Steyerm.) A. Pool, comb. nov. Basionym: *Rhamnus acuminata* Maguire & Steyerm., Mem. New York Bot. Gard. 51: 121. 1989. TYPE: Venezuela. Amazonas: Cerro de la Neblina, Cañon Grande, SSW of Cumbre Camp, 1050–1150 m, 25 Dec. 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 42496* (holotype, NY not seen, image, photo; isotypes, COL not seen, image, K not seen, image, MO, US not seen, image, VEN, not seen, image).

Maguire and Steyermark (1989) published three new species of *Rhamnus* from Cerro Neblina, two of which are considered herein as slight morphological variants of the same species, as *Frangula neblinensis* (Maguire & Steyerm.) A. Pool. Their third species, *F. acuminata*, initially seemed to represent another variant with leaves longer (13.5–18 × 5.5–7.2 cm vs. 5–9.5 × 2.5–5 cm in *F. neblinensis*) and less coriaceous (membranaceous with tertiary venation more or less flat on both surfaces vs. coriaceous and tertiary venation sulcate adaxially and more or less strongly elevated abaxially), variation that might have reflected population differences due to the collection of *F. acuminata* at slightly lower elevations (780–1500 m vs. 1600–2000 m in *F. neblinensis*). However, in addition to the leaf differences, the flowers also distinguish the species in that in *F. acuminata* the hypanthial width is equal to the floral length and the sepals are smaller than the hypanthi-

um while in *F. neblinensis* the hypanthial width is 2/3 the length of the flower and the sepals are about equal to the length of the hypanthium.

Frangula acuminata is sometimes confused with *F. ulei* (Pilg.) Grubov [≡ *Rhamnus ulei* Pilg.] from Guyana and Bolívar, Venezuela. The latter species differs in its smaller flowers (1.7–2 mm vs. ca. 2.5 mm in *F. acuminata*), with the hypanthium densely dull brown tomentose (vs. sparse, appressed ferrugineous indument), the ovary pubescent (vs. glabrous), and the inflorescences sessile and consistently without peduncle (vs. the inflorescences either with or without peduncle).

2. Frangula breedlovei (L. A. Johnst. & M. C. Johnst.) A. Pool, comb. nov. Basionym: *Rhamnus breedlovei* L. A. Johnst. & M. C. Johnst., Fl. Neotrop. 20: 52. 1978. TYPE: Mexico. Chiapas: Mpio. Chamula, SE side of Zontehuitz near summit, 2850 m, 30 July 1964, *D. E. Breedlove 6724* (holotype, MICH; isotypes, ENCB not seen, F).

Frangula breedlovei is unusual in being one of only four species of *Frangula* studied (i.e., *F. oreodendron* (L. O. Williams) A. Pool, *F. granulosa*, and *F. goudotiana* (Triana & Planch.) Grubov s. str.), with a hypanthium that is noncircumscissile, with the sepals, petals, and stamens tardily deciduous from the rim of the hypanthium. This condition more typically occurs in *Rhamnus*, whereas the hypanthium is otherwise circumscissile with the sepals, petals, and stamens lost with the upper half of the hypanthium for other *Frangula*. Nonetheless, *F. breedlovei*, *F. oreodendron*, *F. granulosa*, and *F. goudotiana* s. str. all share the most compelling characteristics separating *Frangula* from *Rhamnus*: bud scales absent, pyrenes indehiscent, and seeds smooth with a thickened cartilaginous basal rostrum exserted through the base of the pyrene. In addition, recent molecular work that included one of these species, *F. granulosa* (Bolmgren, 2013, pers. comm.), strongly supports its placement in this genus.

3. Frangula capreifolia (Schltdl.) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 278. 1949, as "caprifolia." Basionym: *Rhamnus capreifolia* Schltdl., Linnaea 15: 464. 1841, as "capreaefolia." TYPE: Mexico. Veracruz: in saxosis Malpays de Naulingo, *C. J. W. Schiede s.n.* (lectotype, designated by Johnston & Johnston [1978: 32], HAL-21748 not seen, image; isolectotype, W not seen).

3a. Frangula capreifolia (Schltdl.) Grubov var. **capreifolia.**

Rhamnus capreifolia var. *matudae* L. A. Johnst. & M. C. Johnst., Fl. Neotrop. 20: 33. 1978, as "capraeifolia var. matudai," syn. nov. TYPE: Mexico. Veracruz: Encinal, Maltrata, 12 May 1937, *E. Matuda 1383* (holotype, NY; isotypes, A, F, K not seen, image, MICH, MO, NA not seen).

In the original protologue of *Rhamnus capreifolia*, Schlechtendal included specimens made at four localities each with collector and corresponding month and phenological state. Grubov (1949: 278) indicated the type as made by *Schiede* in "sylvis Jalapensibus," one of the original collectors and syntype localities. However, at HAL there are two collections of *Schiede* with this collection information (HAL-105597 and HAL-21523). Later, Johnston and Johnston (1978: 32), without discussion, cited as the type *Schiede s.n.* (HAL-21748), "in saxosis Malpays de Naulingo, prope Jalapa, fl, Apr 1829," another collection (or collections) cited by Schlechtendal. There are two collections of Schiede at HAL made at this locality in April, both in flower (HAL-107596, also in fruit), but only one with the accession number 21748 and it can unambiguously be accepted as the lectotype.

Johnston and Johnston (1978: 30) separated *Rhamnus capreifolia* var. *matudae* from the typical variety based on the "macroscopically conspicuous dense lateral pubescence" of the major veins on the abaxial leaf surfaces of variety *matudae* versus the absence of this pubescence in the typical variety. However, I found this character to be variable in *Frangula capreifolia* var. *capreifolia* throughout its range (eastern Mexico, Tamaulipas to eastern Oaxaca and Veracruz [Johnston & Johnston, 1978]) as well as variable in other *Frangula* studied (*F. breedlovei*, both varieties of *F. discolor* (Donn. Sm.) Grubov, *F. mucronata* (Schltdl.) Grubov, *F. pendula* A. Pool, and *F. pringlei* (Rose) Grubov). Since no other characters were found that could be used to recognize *F. capreifolia* var. *matudae*, the name is synonymized to the autonym.

3b. Frangula capreifolia var. **grandifolia** (M. C. Johnst. & L. A. Johnst.) A. Pool, comb. nov. Basionym: *Rhamnus capreifolia* var. *grandifolia* M. C. Johnst. & L. A. Johnst., Fl. Neotrop. 20: 34. 1978, as "capraeifolia var. grandifolia." TYPE: Mexico. Chiapas: Rancho Phoenix, Monserrate, 1 May 1926, *C. A. Purpus 10201* (holotype, M not seen; isotype UC, not seen).

Rhamnus pompana M. C. Johnst. & L. A. Johnst., Fl. Neotrop. 20: 38. 1978, syn. nov. TYPE: Mexico. Veracruz: near Jalapa, 31 Mar. 1899, *C. G. Pringle*

8079 (holotype, M not seen; isotypes, A not seen, BM not seen, image, E not seen, image, F not seen, image, K not seen, image, HBG not seen, image, L not seen, LL not seen, image, MICH not seen, image, MO, NY, RSA not seen, image, TEX not seen, UC not seen, U, not seen, W not seen).

Johnston and Johnston (1978) also cited and annotated as an isotype a specimen of *C. A. Purpus 10201* at GH, but the date on this collection is April rather than May as noted for the holotype. As Purpus was casual in recording collection dates and did not use chronological collection numbers, assigning the same number to collections of what he believed to be the same taxon regardless of when they were collected (Sousa, 1969), it is not possible to know if this is an actual isotype or from a separate gathering.

Johnston and Johnston (1978) apparently segregated *Rhamnus pompana*, which they recognized from Hidalgo and Veracruz in Mexico, from *R. capreifolia* var. *grandifolia*, based on the smaller leaf size and flowers. However, flowers from the type and other specimens cited by Johnston and Johnston, as seen in this study (2–3 mm), fit easily into the range of *Frangula capreifolia* var. *grandifolia* (2–3.5 mm) and the leaves of the type and other specimens as indicated above (5–10 × 2.5–4.5 cm) do fit within the lower range for other specimens of *F. capreifolia* var. *grandifolia* (total range, 5–20 × 2.5–8.5 cm). No characters were found to separate *R. pompana* from *F. capreifolia* var. *grandifolia*, which is found in Mexico (Hidalgo [e.g., *J. D. Flores M. 235*, MO], Veracruz [e.g., *M. Chazaro B. & P. Sánchez 2209*, MO], Puebla [e.g., *A. J. Sharp 45307*, MO], Oaxaca [e.g., *R. Torres C. & C. Martínez R. 4851*, MO], and Chiapas [e.g., *A. Reyes-García et al. 1590*, MO]), Guatemala (e.g., *E. Contreras 4873*, MO), El Salvador (e.g., *K. J. Sidwell et al. 824*, MO), and Costa Rica (e.g., *G. Rivera 382*, MO).

4. Frangula chimalapensis (R. Fernández) A. Pool, comb. nov. Basionym: *Rhamnus chimalapensis* R. Fernández, Polibotanica 1: 4. 1996. TYPE: México. Oaxaca: San Miguel Chimalapa, arroyo El Caracol, donde desemboca el Río Portamonedas, ca. 1 km al NW de Congregación Benito Juárez, ca. 39 km al N de San Pedro Tepanatepec, 16°43′N 94°09′W, 950 m, *S. Maya 521* (holotype, ENCB not seen; isotypes, CHAPA not seen, MO).

Fernández N. (1996) provided a key separating *Frangula chimalapensis* from the similar *F. palmeri* (S. Watson) Grubov on the basis of leaf size (blade usually greater than 8 cm vs. usually less than 8 cm in *F. palmeri*, petiole 8–10 mm vs. 2–5 mm), number of flowers per inflorescence (3 to 5 vs. 5 to 10), and fruit size (5–7 mm vs. 7–8 mm). To this can be added that in fruit the pedicels of this species are approximately equal in length to the subtending petioles, while in *F. palmeri* the pedicels are twice as long as the petioles.

5. Frangula chimantensis (Steyerm. & Maguire) A. Pool, comb. nov. Basionym: *Rhamnus chimantensis* Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 451. 1967. TYPE: Venezuela. Bolívar: Chimantá Massif, E-central portion of summit of Apácara-tepuí, 2450–2500 m, 21–22 June 1953, *J. A. Steyermark 75946* (holotype, NY not seen, image; isotypes, MO-2012040, MO-2011382, VEN not seen, image).

Rhamnus chimantensis was described from and is endemic to the Guayana region of Venezuela. The species was later treated in Johnston and Johnston (1978) as a synonym of a variable *R. goudotiana* Triana & Planch. [≡ *Frangula goudotiana* (Triana & Planch.) Grubov]. Now recognized as *F. chimantensis*, the species differs from *F. goudotiana* in its unusual inflorescence, which is a pseudo-raceme simple or once branched at the base with each flower subtended by a large and persistent bract, the stipules persistent after the leaves are lost, and the upper portion of the hypanthium, with sepals, stamens, and petals attached, circumscissile and lost early in fruit development. This is in contrast to *F. goudotiana* with the inflorescence a fascicle of flowers with the bracts restricted to the base of the fascicle, the stipules lost before or with the dehiscence of the leaves, and the hypanthium not circumscissile, with the floral perianth and androecium lost independently and late in fruit development. Triana and Planchon (1872) cited in the protologue of *R. goudotiana* another collection, *Triana*, but without specifying a collection number. Johnston and Johnston (1978: 57) include in exsiccate *Triana 3529* (BM, NY, US) and note that this is the syntype not chosen by them (1978: 56) as the lectotype for *F. goudotiana*, *J. Goudot s.n.* (P). *Triana 3529* (based on observations from the duplicate at MO and the image of the duplicate at P) differs from the description in the original protologue in having the undersurface of the leaf the same color as the veins (brown-green) versus in the protologue: "subtus pallidioribus fusco-venosis [below paler (than the upper surface) dark brown veined]" (Triana & Planchon, 1872: 379). *Triana 3529* also differs from the *Goudot* specimen in having a circumscissile hypanthium. I have seen a number of specimens of both forms of *F. goudotiana* and suggest that further study may prove them to be independent species.

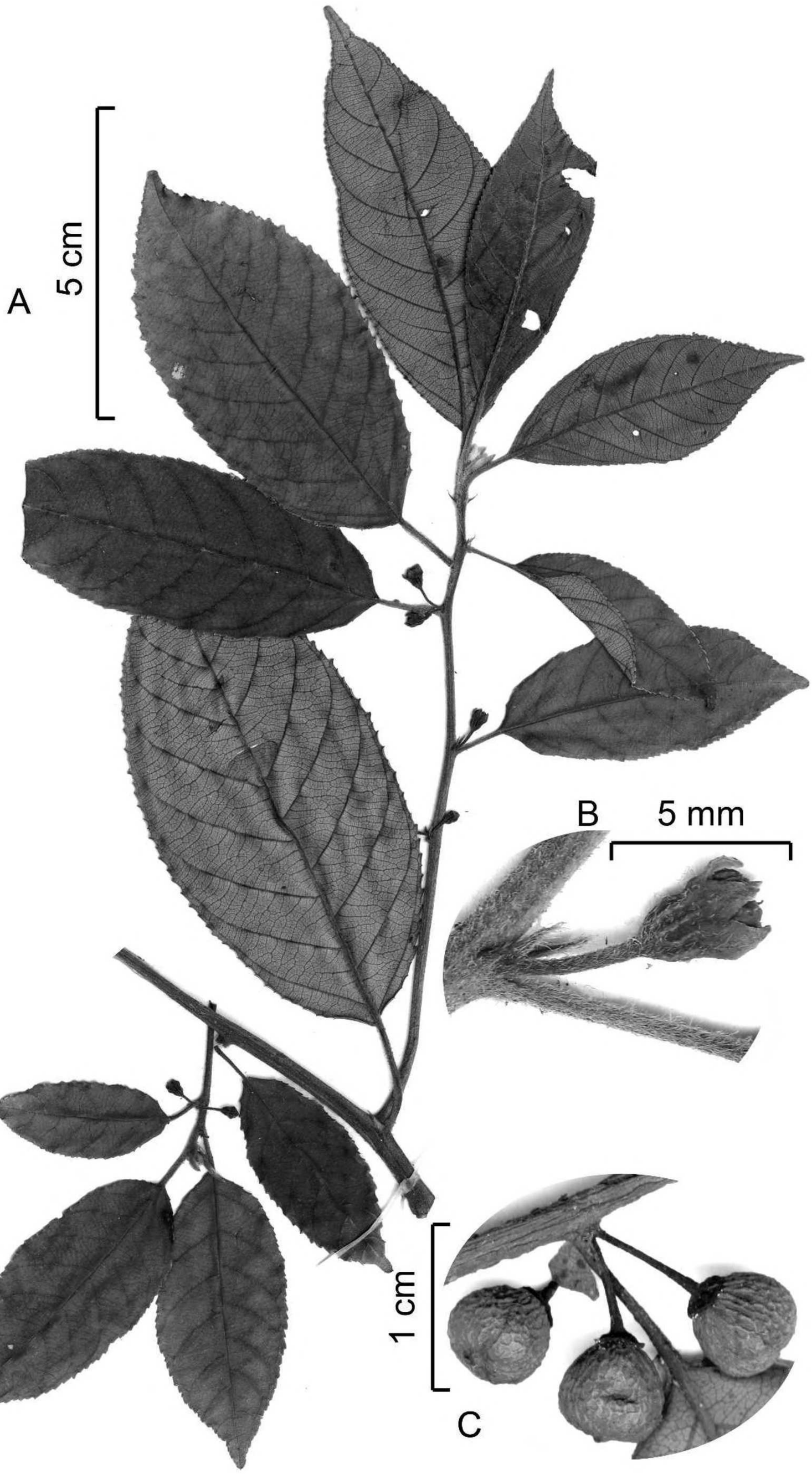

Figure 2. *Frangula circumscissa* A. Pool. —A. Flowering branch. —B. Flower in leaf axil. —C. Infructescence in leaf axil. A, B taken from the holotype *L. Acosta & V. Ramírez 563* (MO); C from *G. A Mora V. 414* (MO).

6. Frangula circumscissa A. Pool, sp. nov. TYPE: Costa Rica. Cartago: Paraíso, Parque Nacional Tapantí, Macizo de La Muerte, cuenca del Reventazón, colecta a orilla de calle desde el cruce de Río Humo al Túnel, 9°42′10″N 83°47′20″W, 1700 m, 8 Mar. 2000, *L. Acosta & V. Ramírez 563* (holotype, MO isotype, INB not seen). Figure 2.

Diagnosis. *Frangula circumscissa* A. Pool is similar to *F. oreodendron* (L. O. Williams) A. Pool, differing in membranaceous leaves and the hypanthium narrower and circumscissile.

Small trees or shrubs, 2–6 m, young branches densely tomentose or with abundant appressed and ascending, pale red trichomes. Leaves with blades 6.2–15.5 × 2.3–5 cm, elliptic, membranaceous, both surfaces of similar color, 8 to 10 pairs of lateral veins, these at 45° angles to midrib, adaxial surface with trichomes, appressed to ascending, mainly on midrib and lateral veins, abaxial surface glabrous or with trichomes restricted to midrib and lateral veins, these appressed to ascending or somewhat spreading, lamina base cuneate, sometimes inequilateral, blade margin nearly flat to recurved, serrate to serrulate with 5 to 8 teeth/centimeter, apex acute to short-acuminate or obtuse and then shortly cuspidate, tip mucronate; stipules persistent into early fruit, 2–3.5 mm; petiole 7–30 mm. Inflorescence a sessile fascicle with 1 to 4 flowers; flowers on pedicels 4–8 mm, 1/2–3/4 length of subtending petiole (of similar size, 1/3–3/4 length of petiole in fruit). Flowers 2.75–3.5 mm, with the hypanthium narrowly funnelform to tubular, 2–2.5 × 2.25–2.75 mm, hypanthium width ca. 3/4 to nearly equaling the length of the flower, with sparse to scattered trichomes that are appressed and ascending, with circumscissile dehiscence, the sepals, petals and stamens lost early with the upper portion of the hypanthium; sepals 0.75–1.25 mm long and wide, 1/2 hypanthium in length, erect; petals 1–1.5 mm long and wide, weakly apically bi-lobed, glabrous, apically exserted; stamens with filaments 0.6–0.75 mm, anthers 0.4–0.6 mm, not visible free from petals; ovary glabrous, style 1–1.2 mm, stigma 3-lobed. Young fruits 2- to 4-fascicled, glabrous, globose, lines not apparent; all sepals, petals and stamen filaments rapidly lost, hypanthium remnant 1–1.25 × 3–3.5 mm, not angled; pyrenes not seen.

Phenology. *Frangula circumscissa* has been collected in flower in March and September.

This new species, known only from Costa Rica, has previously been most often confused with *Frangula oreodendron* of Costa Rica and Panama. The latter differs in having leaves with firm texture (vs. membranaceous in *F. circumscissa*) and hypanthia that are broadly campanulate, (1.25–)1.5–2.75 × (2.3–)3–4.5 mm, and not circumscissile, the sepals, petals, and stamens tardily and separately lost in fruit. In *F. circumscissa*, the hypanthia are narrowly funnelform to tubular, 2–2.5 × 2.25–2.75 mm, and circumscissile, with the sepals, petals, and stamens lost with the dehiscence of the apical portion of the hypanthium. The new species is also similar to *F. mucronata* found to the north, from Mexico, Guatemala, and El Salvador. The latter differs in its leaves usually narrower (1.5–3 cm vs. 2.3–5 cm in *F. circumscissa*), often pilose, with acuminate apices on usually smaller petioles (3.5–10 mm vs. 7–30 mm in *F. circumscissa*), and the pedicels often equal or slightly longer than the subtending petioles in flower and especially in fruit. In the new species, the pedicels are shorter than the subtending petioles in flower and fruit. While mature pyrenes of *F. circumscissa* were not observed, the immature pyrenes are of the type typical of the genus, open at the base with the horny base of seeds exserted.

Distribution. This species is apparently endemic to north central Costa Rica, where it has been collected between 1300 and 2000 m.

IUCN Red List category. The new species is assessed as DD or Data Deficient, according to IUCN (2012) criteria. *Frangula circumscissa* is known from only six collections from five localities in north central Costa Rica, made between 1300 and 2000 m in elevation. The EOO is estimated at ca. 2500 km² and the minimum AOO is ca. 20 km².

Paratypes. COSTA RICA. **Alajuela:** San Ramon, Reserva Biol. Monteverde, Cordillera de Tilarán, Valle del Río Peñas Blancas, 10°19′12″N 084°46′12″W, 22 July 1993, *E. Bello C. 5162* (CR not seen, MO); Los Angeles, Reserva Biol. Alberto M. Brenes, sendero entre la Estación y Volcán Muerto, 10°11′50″N 084°37′00″W, 15 Sep. 1994, *G. Herrera Ch., V. Mora & H. Perez Z. 7308* (CR not seen, F). **Cartago:** Paraiso, Parque Nac. Tapantí, Valle del Reventazón, Sector Dos Amigos, Sendero Rancho Negro, 09°42′10″N 083°47′20″W, 9 Dec. 1994, *G. A. Mora V. 414* (INB not seen, MO). **Heredia:** Yerba Buena, NE of San Isidro, 10°01′12″N 084°00′36″W, 28 Feb. 1926, *P. C. Standley & J. Valerio R. 49997* (US); original label lost "**Puntarenas** & **Alajuela:** Monteverde Reserve, 2–5 km E and SE of Monteverde, 10°18′N 084°06′W," s.d., *V. J. Dryer s.n.* (F).

7. Frangula darienensis A. Pool, sp. nov. TYPE: Panama. Darien: Cerro Tacarcuna massif, W ridge, vic. of summit camp, lower montane wet forest, 1500–1600 m, 5 Feb. 1975, *A. Gentry & S. Mori 14160* (holotype, MO). Figure 3.

Diagnosis. *Frangula darienensis* A. Pool is similar to *F. pubescens* (Ruiz & Pav.) Grubov, differing in its persistent stipules, the oblanceolate to narrowly oblanceolate, membranaceous leaves drying on adaxial surface with bluish cast, and the indumentum of the abaxial surface including compound trichomes with tortuous arms from a common base, the hypanthium with off-white, appressed, ascending trichomes, and petals minutely apically retuse.

Treelet, ca. 4 m, young branches sparsely to densely tomentose with pale gold to red-gold

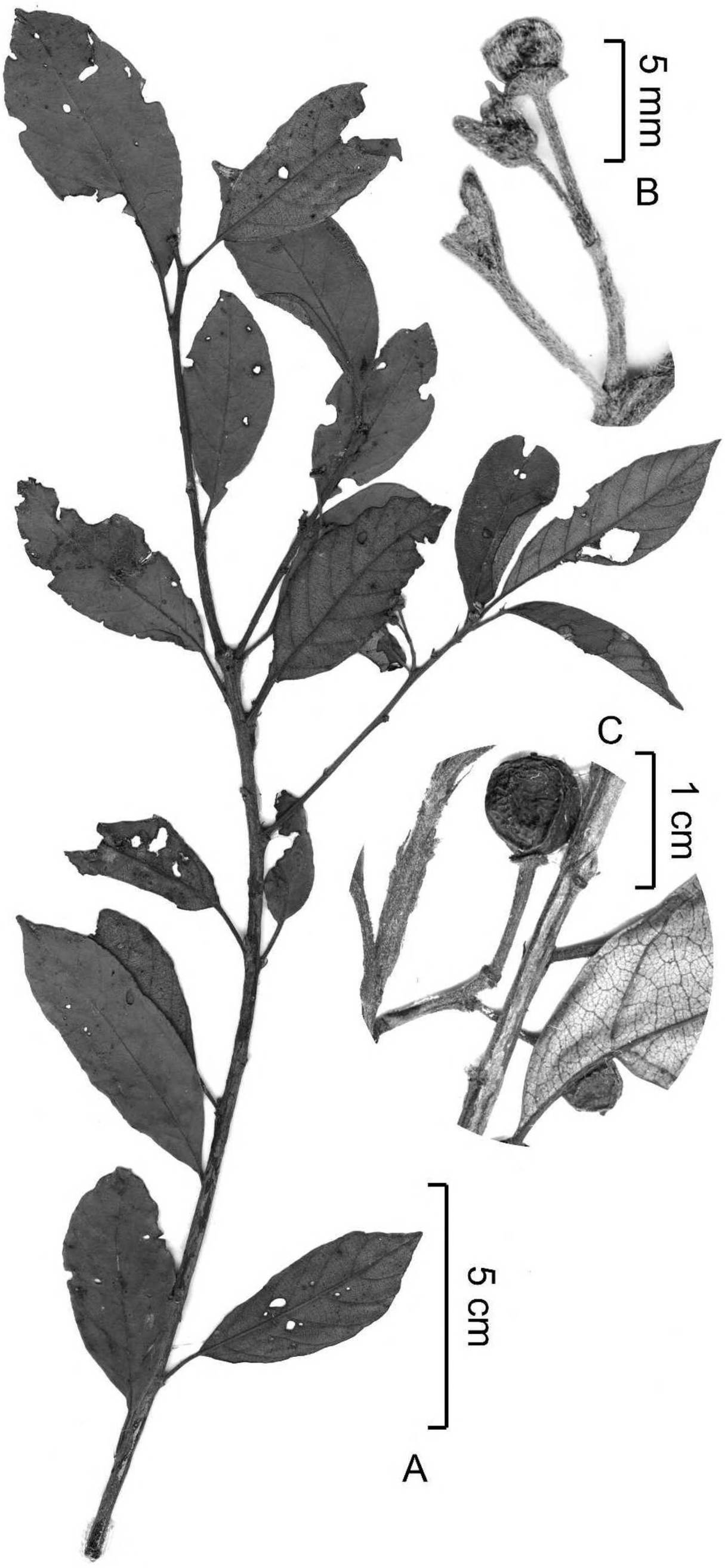

Figure 3. *Frangula darienensis* A. Pool. —A. Flowering branch. —B. Inflorescence in leaf axil with one flower and one immature fruit. —C. Infructescence in leaf axil, with two immature fruits. A, B taken from the holotype *A. Gentry & S. Mori 14160* (MO); C from *A. Gentry & S. Mori 13982* (MO).

trichomes. Leaves with blades 5–10 × 2–3.5 cm, oblanceolate to narrowly oblanceolate, membranaceous, bicolored, with the adaxial surface drying with bluish cast, 6 to 10 pairs of lateral veins, these at 45° angles to midrib, adaxial surface with appressed, ascending to spreading trichomes on midrib and lateral veins, otherwise glabrous, abaxial surface with all orders of venation with numerous trichomes appressed and ascending to spreading, the trichomes simple and solitary and in small tufts, and compound

with tortuous arms from a common stalk, lamina base cuneate to attenuate, sometimes inequilateral, blade margin flat, serrulate or with teeth overlapping on adaxial surface, with 4 to 6 teeth/centimeter, apex obtuse then cuspidate, tip mucronate or not; stipules persistent at least into early fruiting, 2.5–3.5 mm; petioles 7–10 mm. Inflorescence a sessile fascicle, a pedunculate cyme, or a pedunculate compound cyme, each fascicle with 1 or 2 flowers; peduncle 0–7 mm, slightly to probably much shorter than subtending petiole (similar in fruit); flowers on pedicels ca. 4.25 mm, 2/3 the length of peduncle when present, pedicels ca. 2/3 the length of subtending petiole (8–10 mm in fruit, slightly longer to 10 times longer than peduncle (when present) and 5/4 the length of subtending petiole). Flowers ca. 3.2 mm, with the hypanthium tubular, ca. 1.8 × 2.1 mm, hypanthium width ca. 2/3 the flower length, with numerous appressed and ascending trichomes, with circumscissile dehiscence, the sepals, petals and stamens lost early with upper portion of hypanthium; sepals ca. 1.5 × 1 mm, slightly shorter than the hypanthium length, erect; petals ca. 0.7 × 1 mm, minutely apically retuse, abaxially pubescent on midrib, exserted; stamens with filaments not known, anthers ca. 0.5 mm, not visible free from petals; ovary with dense, long trichomes, style not known, stigma not known. Young fruits solitary, with numerous trichomes, obovoid, lines not observable; all sepals, petals and stamen filaments rapidly lost with circumscissile dehiscence of hypanthium, hypanthium remnant 0.5–0.75 × 2.5–2.8 mm, not angled; pyrenes not known.

Phenology. *Frangula darienensis* has been collected in flower in February.

Frangula darienensis is known from only two collections from Cerro Tacarcuna, Darien, Panama. Only one flower was seen, which was not dissected. The subtending leaf was lost from one of the two immature fruits observed, and it was not possible to see the peduncle of the remains of a third immature fruit. With its tubular hypanthium with erect sepals, often pedunculate inflorescence, and pubescent ovary, this species is morphologically closest to the Andean species *F. pubescens* (Ruiz & Pav.) Grubov, which was treated by Johnston and Johnston (1978) as part of their concept of an extremely variable *Rhamnus sphaerosperma* var. *pubescens* (Reissek) M. C. Johnst. (cf. discussion for *F. polymorpha* Reissek and *F. pubescens*). *Frangula darienensis* differs from *F. pubescens* in its retained stipules (vs. caducous in flower in *F. pubescens*), the hypanthium with off-white, appressed, ascending trichomes (vs. ferruginous tomentose), the petals minutely apically retuse (vs. strongly bi-lobed) and the oblanceolate to narrowly oblanceolate, membranaceous leaves drying with the adaxial surface with bluish cast and the trichomes on the abaxial blade surface including compound forms with tortuous arms from a common base. In *F. pubescens* the leaves are usually wider, elliptic, firm to subcoriaceous, drying green to brown, and rarely nearly black, with only simple solitary and tufted trichomes observed.

Distribution. The new species is apparently endemic to Cerro Tacarcuna, Darien, Panama, where it has been collected in elfin or lower montane wet forest between 1500 and 1850 m in elevation.

IUCN Red List category. *Frangula darienensis* is assessed as DD or Data Deficient, according to IUCN (2012) criteria. As this new species is known from only two collections made at the type locality, the EOO and the minimum AOO were not calculated.

Paratype. PANAMA. **Darien:** Top of W peak of Cerro Tacarcuna massif, 28 Jan. 1975, *A. Gentry & S. Mori 13982* (MO-2294408, MO-3100499).

8. Frangula discolor (Donn. Sm.) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 274. 1949. Basionym: *Rhamnus capreifolia* var. *discolor* Donn. Sm., Bot. Gaz. 18: 200. 1893, as "capreaefolia." *Rhamnus discolor* (Donn. Sm.) Rose, Contr. U. S. Natl. Herb. 8: 51. 1903, non *Rhamnus discolor*, Lesq., Rep. (Annual) U. S. Geol. Geogr. Surv. Territ. 6: 398. 1873. Replacement name: *Rhamnus sharpii* M. C. Johnst. & L. A. Johnst., Fl. Neotrop. 20: 74. 1978. Guatemala. Alta Verapaz, Cobán, 4300 ft., Aug. 1885, *H. von Türckheim 710* (holotype, US; isotypes, F, NY, US).

8a. Frangula discolor (Donn. Sm.) Grubov var. **discolor**.

8b. Frangula discolor var. **mesoamericana** (L. A. Johnst. & M. C. Johnst.) A. Pool, comb. nov. Basionym: *Rhamnus sphaerosperma* var. *mesoamericana* L. A. Johnst. & M. C. Johnst., Fl. Neotrop. 20: 64. 1978. TYPE: Guatemala. [in woods at Acetuna] near Guatemala, July 1860, *S. Hayes s.n.* (holotype, US-355630; isotypes, F, F fragm. at GH).

This variety was originally described within the species *Rhamnus sphaerosperma* Sw. *Frangula discolor* var. *mesoamericana* is similar to *F. discolor* var. *discolor* and both varieties differ from *F. sphaerosperma* (Sw.) Kartesz & Gandhi (endemic to Jamaica and Cuba) in the early caducous stipules (vs.

retained stipules in *F. sphaerosperma*), the pedicels often longer, 1.5–7 mm in flower and 2.5–14 mm in fruit (vs. 1.5–3 mm and 1.5–4 mm), the hypanthium more or less tubular (vs. campanulate), the petals and anthers only apically exserted (vs. well-exserted), and by the presence of appressed sessile stellate trichomes on the abaxial surface of the leaves (vs. lacking this type of trichome). *Frangula discolor* var. *mesoamericana* differs from typical *F. discolor* only in the glabrous ovaries and fruits of the former and pubescent ovary and fruits of the latter. *Frangula discolor* itself was first published as *R. capreifolia* var. *discolor* Donn. Sm. Johnston and Johnston (1978) treated this taxon at the species level, with the replacement name *R. sharpii* M. C. Johnst. & L. A. Johnst. *Frangula discolor* differs from *F. capreifolia* in the presence of appressed sessile stellate trichomes on the abaxial leaf surface (vs. absent in *F. capreifolia*), by the hypanthium more or less tubular and densely tomentose (vs. campanulate and sparsely to abundantly pilose), and by the sepals erect to spreading (vs. spreading to recurved).

Frangula discolor var. *mesoamericana* is known from Chiapas, Mexico (e.g., *D. E. Breedlove 11188*, MICH) to northern Nicaragua (e.g., *J. Pipoly 5151*, TEX) and has a smaller known geographic range than the typical variety, which ranges as far north as Colima, Mexico (e.g., *A. C. Sanders et al. 10713*, MO), and south to northern Panama (e.g., *S. Mori & J. Kallunki 5620*, MO). *Frangula discolor* var. *mesoamericana* is most common in Honduras (e.g., *P. House & R. Andino 970*, MO), while *F. discolor* var. *discolor* is most common in Chiapas, Guatemala, Costa Rica, and northern Panama, and has not been collected in Honduras.

9. Frangula grandiflora A. Pool, sp. nov. TYPE: Honduras. Lempira: Norte Río Arcágual, filo N del Camp. Arcágual, 13 km al SO de Gracias, en el Parque Nac. de Celaque, 14°34′N 88°41′W, 2700 m, 15 May 1992, *D. Mejía & T. Hawkins 101* (holotype, MO; isotypes, EAP not seen, HEH not seen, MEXU, TEFH not seen, TEX). Figure 4.

Diagnosis. *Frangula grandiflora* A. Pool is similar to *F. capreifolia* var. *grandifolia* (M. C. Johnst. & L. A. Johnst.) A. Pool, differing in the larger flowers (4–5.75 mm), with the hypanthium funnelform, longer pedicels (10–13 mm in flower, 12–19 mm in fruit), and the leaves subcoriaceous.

Trees or shrubs, 4.5–15 m, young branches densely tomentose to pilose, with red-gold trichomes. Leaves with blades 7.6–20.7 × 2.6–7.5 cm, oblong or elliptic, subcoriaceous, both surfaces of similar color, 8 to 11 pairs of lateral veins, lateral veins at 45° angles to midrib, adaxial surface glabrous or with a few appressed trichomes on midrib, or the midrib and lateral veins densely pilose, abaxial surface with trichomes on midrib and lateral veins and sometimes on all venation, the trichomes mixed, with small and longer tortuous and tufted and sometimes also longer, straight and spreading, solitary or in tufts of 2, without macroscopically conspicuous concentration of trichomes along sides of midrib and/or in angles of lateral veins, lamina base cuneate or rounded, margin strongly recurved with 3 or 4 teeth/centimeter, the teeth usually consisting only of apical glands, less frequently weakly serrulate, blade apex acute or short-acuminate, tip often mucronate; stipules very early caducous, ca. 2 mm; petiole 10–20 mm. Inflorescence a sessile fascicle with 3 to 5 flowers; pedicels 10–13 mm, equal in length to subtending petiole to slightly longer, pedicels in fruit 12–19 mm, and 3/4 to 3/2 times the length of subtending petioles. Flowers 4–5.75 mm, with the hypanthium funnelform, 2.5–3.25 × 3.2–4.5 mm, hypanthium width less than length of flower, densely tomentose, with circumscissile dehiscence, the sepals, petals, and stamens lost early with upper portion of hypanthium; sepals 1.5–2.5 × 1.25–1.5 mm, shorter than hypanthium, erect to spreading; petals ca. 1.2 mm long and wide, slightly apically bi-lobed, abaxially minutely puberulent medially, slightly exserted; stamens (perhaps young) with filaments ca. 0.9 mm, anthers ca. 0.8 mm, not visible free from petals; ovary with dense long trichomes, style ca. 1 mm, stigma 3-lobed. Young fruits 1- or 2-fascicled, with numerous trichomes, globose to obovoid, lines not noticeable; all sepals, petals or stamen filaments rapidly lost with circumscissile dehiscence of upper hypanthium, hypanthium remnant 0.75–1.5 × 3–3.25 mm, not angled; pyrenes 3, ca. 6 × 5 mm.

Phenology. *Frangula grandiflora* was collected in flower only in the month of May.

The new species is unusual in its robust pedicels and large flowers. In the Neotropics only *Frangula longistyla* has a flower that is similar in size (up to 4.75 mm) with *F. grandiflora* (4–5.75 mm). *Frangula longistyla* differs in having a tubular hypanthium (vs. funnelform in *F. grandiflora*), sporadically retained stipules (vs. consistently early caducous), and membranaceous leaves (vs. subcoriaceous). *Frangula capreifolia* var. *grandifolia*, with its early caducous stipules, sessile fascicles, and pubescent ovaries and fruits, is the taxon perhaps most superficially similar to *F. grandiflora*. *Frangula capreifolia* var. *grandifolia* differs in its membranaceous leaves (vs. subcoriaceous in *F. grandiflora*), pedicels 2.5–10

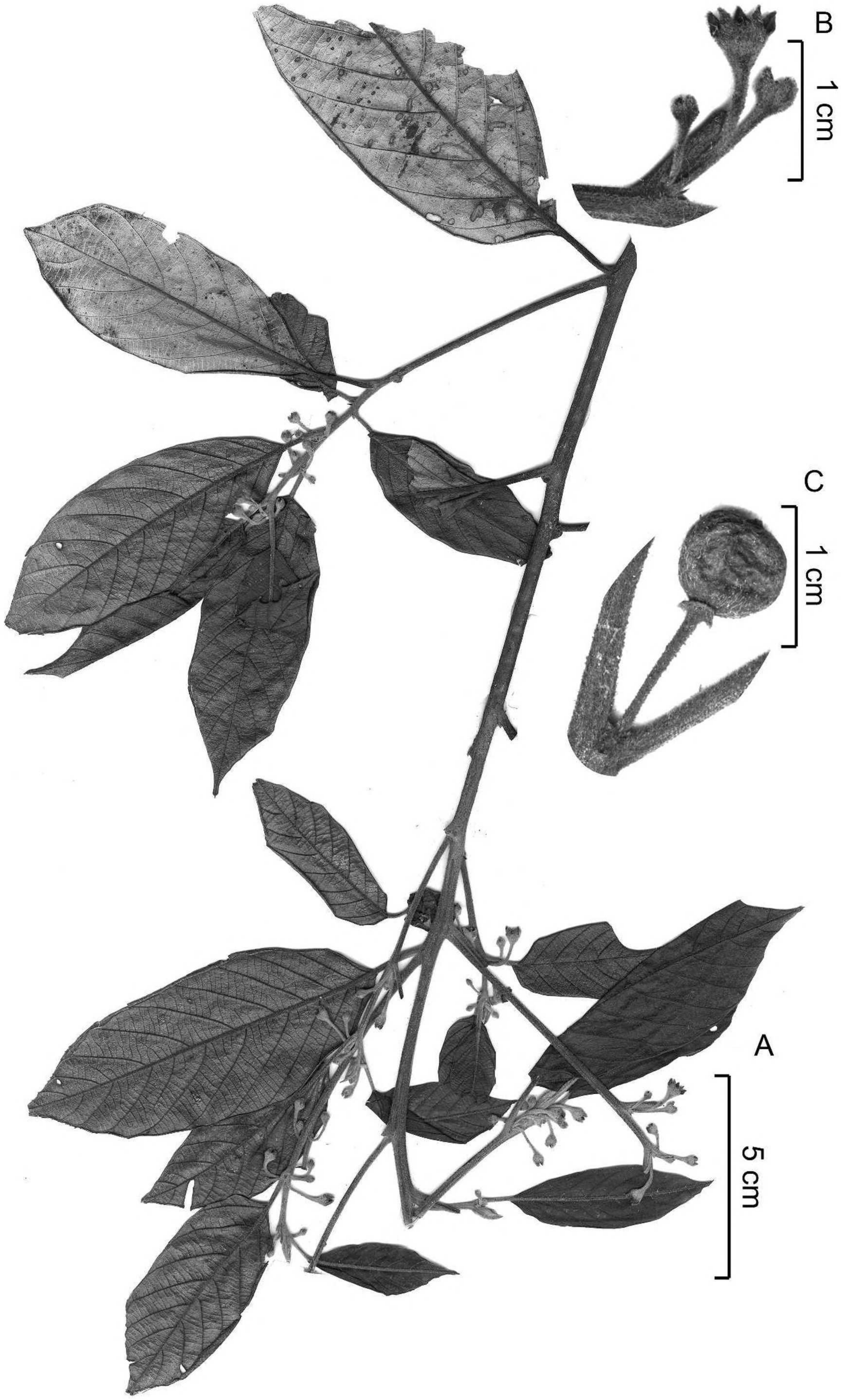

Figure 4. *Frangula grandiflora* A. Pool. —A. Flowering branch. —B. Inflorescence in leaf axil. —C. Immature fruit in leaf axil. A, B taken from the holotype *D. Mejía & T. Hawkins 101* (MO); C from *D. E. Breedlove & B. Bartholomew 55909* (CAS).

mm in flower and in fruit (vs. 10–13 in flower and 12–19 mm, in fruit) and smaller flowers (2–3.5 mm vs. 4–5.75 mm) and campanulate hypanthia (vs. funnelform).

Distribution. This new species is known from only two localities. *Frangula grandiflora* is described from the type location within the Parque Nacional de Celaque, Lempira, Honduras, and is also known from

the Cerro Mozotal, Chiapas, Mexico. It has been collected in cloud forest between 2500 and 2700 m in elevation.

IUCN Red List category. *Frangula grandiflora* is assessed as DD or Data Deficient, according to IUCN (2012) criteria. The new species is known from only three collections from two localities, and the EOO is estimated at 2100 km², AOO at 12 km². Two of the collections were made in protected areas within the Parque Nacional de Celaque in Honduras.

Paratypes. MEXICO. **Chiapas:** Mpio. of Motozintla de Mendoza, near summit of Cerro Mozotal, 24 Nov. 1981, *D. E. Breedlove & B. Bartholomew 55909* (CAS, TEX). HONDURAS. **Lempira:** Río Arcágual, Parque Nac. de Celaque, 14°40′N 88°42′W, 15 May 1992, *T. Hawkins, P. House, B. Allen & R. Moran 78* (EAP not seen, HEH not seen, MO-4598110, MO-4634191, TEFH not seen).

10. Frangula hintonii (M. C. Johnst. & L. A. Johnst.) A. Pool, comb. nov. Basionym: *Rhamnus hintonii* M. C. Johnst. & L. A. Johnst., Fl. Neotrop. 20: 42. 1978. TYPE: Mexico [State of Mexico], Temascaltepec, Rincón, 1960 m, 30 July 1932, *G. B. Hinton 1141* (holotype, K not seen; isotypes ASU not seen, BM not seen, image, DBG not seen).

This species, as described by Johnston and Johnston (1978), is known from west central and central Mexico and can have either glabrous or pubescent ovaries and fruits. The flowers are borne in sessile fascicles on pedicels smaller than the subtending leaf petioles. Its most unusual characteristic is the leaf margins which are conspicuously toothed with the teeth irregular in size and shape.

11. Frangula inconspicua A. Pool, sp. nov. TYPE: Mexico. Oaxaca: Mpio. San Felipe Usila, Parteaguas, ladera con exposición S, 3.5 km en linea recta al SE de Santa Cruz Tepetotutla, 17°42′53″N 96°32′12″W, 1050 m, 7 mayo 1994, *P. Osorio H. 159* (holotype, MO; isotype, MEXU not seen). Figure 5.

Diagnosis. *Frangula inconspicua* A. Pool is similar to *F. mucronata* (Schltdl.) Grubov, differing in the pubescent ovary and fruit, consistently persistent stipules, usually smaller flowers, and membranaceous leaves with the adaxial surface drying a darker color than the abaxial surface.

Shrubs and small trees, 1.5–4 m, young branches abundantly to densely covered with appressed to ascending or slightly spreading, off-white to pale red-gold trichomes. Leaves with blades 5–10.2 × 1.5–3.5 cm, elliptic, membranaceous, adaxial surface dark brown or dark green and abaxial surface light green or light brown, (5)6 or 7(8) pairs of lateral veins, these at 45° angles to midrib, adaxial surface with appressed to ascending trichomes on midrib and lateral veins, abaxial surface with sparse to numerous appressed to ascending trichomes on all orders of venation and sometimes sparsely on surface, sometimes with some additional trichomes laterally spreading from midrib, lamina base cuneate to attenuate, margin flat to slightly recurved with 4 to 6 teeth/centimeter, distinctly serrate with teeth curving away from leaf surface to, more frequently, teeth overlapping adaxial surface, often only the apical gland of teeth apparent, blade apex acuminate, tip often slightly mucronate; all or most stipules consistently persisting into fruiting, 1.5–3.5 mm; petiole 3–10 mm. Inflorescence a solitary flower or pair of flowers, rarely a sessile fascicle of 4 flowers; pedicels 2.2–4 mm, (rarely half) ca. equaling length of subtending petiole, 4–6 mm in fruit, 2/3 to slightly longer than subtending petiole. Flowers 2–2.5 mm, with the hypanthium tubular to campanulate, 1–1.5 × 1.75–2.2 mm, hypanthium width 3/4 to equaling the length of flower with abundant trichomes that are appressed and ascending to slightly spreading, with circumscissile dehiscence, the sepals, petals, and stamens lost early with upper portion of hypanthium; sepals 0.75–1 × 0.75 mm, 2/3 to equaling hypanthium in length, erect; petals ca. 0.75 × 0.75–1 mm, strongly apically bi-lobed, glabrous or with trichomes on midrib, slightly apically exserted; stamens with filaments 0.5–0.6 mm, anthers 0.5–0.6 mm, apically visible free from petals; ovary with dense long trichomes, style 0.5–1 mm, stigma 3-lobed. Young fruits solitary, with scattered trichomes, globose, with 3 inconspicuous vertical lines; all sepals, petals and stamen filaments rapidly lost, hypanthium remnant 0.5–1.25 × 2–3 mm, not angled; pyrenes 3, ca. 5 × 4.5 mm.

Phenology. *Frangula inconspicua* was collected in flower in April and May.

This inconspicuous species is most similar to *Frangula mucronata* from which it differs in its pubescent ovary and fruit, the consistently persistent stipules, the usually smaller flowers (2–2.5 mm long), and membranaceous and somewhat bicolored leaves, with the adaxial surface dark brown or dark green and the abaxial light brown or light green. In *F. mucronata*, the ovary and fruit are glabrous, the stipules are inconsistently persistent, the flowers are larger (2.5–3.5 mm long), and the leaves are firm and usually concolorous, yellow-green to yellow-brown on both surfaces. Most of the specimens have been previously identified as *Rhamnus capreifolia* or *R. capreifolia* var. *grandifolia*. *Frangula inconspicua* is

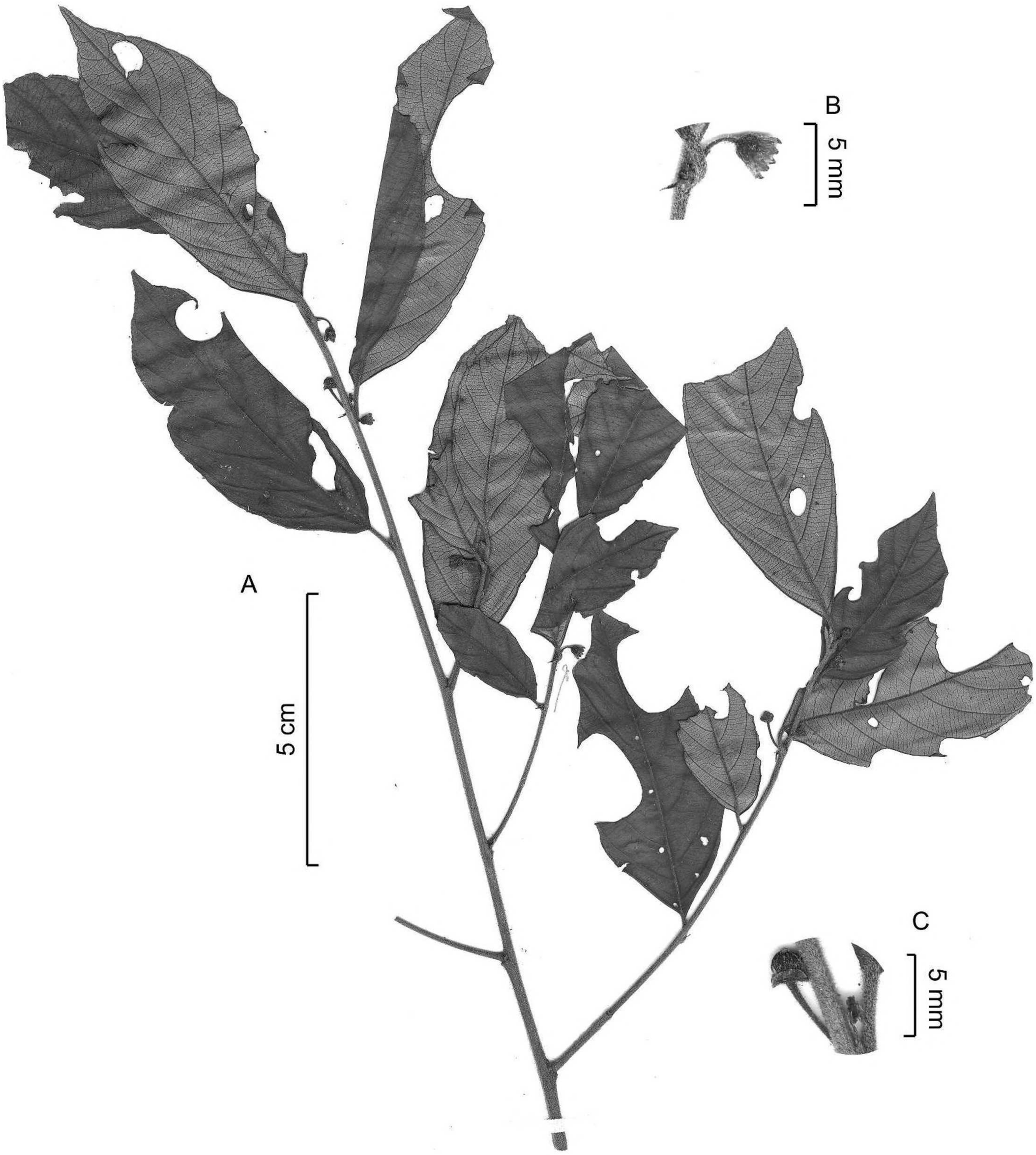

Figure 5. *Frangula inconspicua* A. Pool. —A. Flowering branch. —B. Flower in leaf axil. —C. Immature fruit in leaf axil. A–C taken from the holotype *P. Osorio H. 159* (MO).

similar to *F. capreifolia* var. *grandifolia* in having pubescent ovaries and fruits, but *F. capreifolia* var. *grandifolia* is different in having usually wider leaves (2.8–8.5 cm vs. 1.5–3.5 cm in *F. inconspicua*), with additional pairs of lateral veins (eight to 14 vs. five to eight), rapidly caducous stipules (vs. stipules consistently persistent), the inflorescence often pedunculate (vs. always sessile), flowers in fascicles of six to 20 (vs. flowers solitary or paired, rarely four), flowers with the hypanthium usually wider (2–3.5 mm vs. 1.75–2.2 mm), and sepals spreading to recurved (vs. erect). In fruit, *F. inconspicua* is sometimes confused with *F. longistyla*, which has narrowly elliptic leaves, sporadically retained stipules, and pubescent fruits, one to three per fascicle on pedicels that are often equal to (total range 3/5 to two times) the subtending petiole. However, *F. longistyla* differs from *F. inconspicua* in having lateral veins usually initiating at a wider angle to midrib (rarely 45°, typically 60–80° vs. more consistently 45° in *F. inconspicua*) and tortuous erect trichomes on the venation of the abaxial leaf surface, sometimes very sparse and

limited to midrib (vs. trichomes more or less straight or slightly curved and appressed to ascending). The species are easily separated in flower: *F. longistyla* has flowers 3.5–4.75 mm long (vs. 2–2.5 mm in *F. inconspicua*) with sepals spreading to strongly recurved (vs. erect).

Distribution. The new species has been collected only from Oaxaca, Mexico, with seven of the collections from the municipio San Felipe Usila and one additional collection from Sta. María Chimalapa. *Frangula inconspicua* was collected between 1050 and 1900 m in cloud forest.

IUCN Red List category. *Frangula inconspicua* is assessed as DD or Data Deficient, according to IUCN Red List (2012) criteria. No material of this taxon was received on loan, and, as the MO holdings from Oaxaca are not strong, the EOO and AOO were not calculated.

Paratypes. MEXICO. **Oaxaca:** Juchitán, Sta. María Chimalapa, Puerto de los Duendes, en filo entre Cerro El Quetzal (al NE) y Cerro Salomon (al S), 16°45′30″N 094°11′30″W, 22 July 1985, *T. L. Wendt, M. Ishiki I. & S. Maya J. 5092* (CHAPA not seen, MO); Tuxtepec, Mpio. San Felipe Usila, 7 km S de Santa Cruz Tepetotutla, 17°40′19″N 096°32′31″W, 4 Apr. 1994, *A. Rincón G., C. Gallardo H., S. Espinosa & N. Flores 384* (MEXU not seen, MO), 4.4 km SE de Santa Cruz Tepetotutla, 17°42′10″N 096°32′30″W, 17 Sep. 2004, *A. Rincón G. 3103* (MEXU not seen, MO), 4.8 km SE de Santa Cruz Tepetotutla, 17°41′47″N 096°32′15″W, 23 Nov. 1996, *C. Gallardo H., A. Rincón G., J. Meave del C., F. G. Lorea H. & D. Munn 1958* (MEXU not seen, MO), 5.2 km SE de Santa Cruz Tepetotutla, 17°41′34″N 096°32′07″W, 26 Mar. 1995, *A. Rincón G., C. Gallardo H., E. A. Pérez G., A. Osorio M. & B. Osorio M. 568* (MEXU not seen, MO), 4.5 km SE de Santa Cruz Tepetotutla, 17°42′03″N 096°32′36″W, 27 Nov. 1997, *A. Rincón G., C. Gallardo H., J. Meave del C. & Y. Arellanes C. 818* (MEXU not seen, MO), 24 Nov. 1997, *C. Gallardo H., A. Rincón G., J. Meave del C. & Y. Arellanes C. 2181* (MEXU not seen, MO).

12. Frangula longipedicellata A. Pool, nom. et stat. nov. Replaced name: *Rhamnus sphaerosperma* var. *longipes* M. C. Johnst. & L. A. Johnst., Fl. Neotrop. 20: 62. 1978, non *Frangula longipes* (Merr. & Chun) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 266. 1949. TYPE: Puerto Rico, prope Lares in fruticetis ad Jobos, 29 Jan. 1887, *P. Sintenis 6075* (holotype, M not seen; isotypes, BM not seen, image, GH not seen, K not seen, image, L not seen, MO, NY, P not seen, S not seen, image, W not seen, WU not seen).

When transferring this taxon to *Frangula* at species rank, the name *F. longipes* (Merr. & Chun) Grubov blocks the use of the varietal epithet established by Johnston and Johnston (1978).

Johnston and Johnston (1978) published this taxon at the rank of variety within *Rhamnus sphaerosperma*, but it is here recognized at the species rank, based on the many differences between the two taxa. *Frangula longipedicellata* differs from *F. sphaerosperma* in the hypanthium shape and pubescence (tubular and pilose vs. campanulate and with appressed trichomes in *F. sphaerosperma*), the floral size (3–4 mm, hypanthium width 2/3 the length of flower vs. 1.75–3 mm, and hypanthium width equal to length of flower), the petals and anthers only apically exserted versus well-exserted, and pedicel lengths (5.5–9 mm in flower and 8–15 mm in fruit vs. 1.5–3 mm and 1.5–4 mm). The species have non-overlapping geographic distributions, with *F. sphaerosperma* known from Cuba and Jamaica and *F. longipedicellata* from Hispaniola and Puerto Rico (Johnston & Johnston, 1978).

13. Frangula longistyla (C. B. Wolf) A. Pool, comb. nov. Basionym: *Rhamnus longistyla* C. B. Wolf, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 113. 1938. TYPE: Mexico. Hidalgo: pine forests near Trinidad Iron Works, 30 Apr. 1904, *C. G. Pringle 8897* (holotype, US not seen, image; isotypes, BM not seen, image, CAS not seen, image, MA not seen, image, MO, RSA not seen, image, UC not seen).

This species is easily recognized in flower due to its large flowers (3.5–4.75 mm) with tubular hypanthia and sepals spreading to strongly recurved. In fruit it can be confused with *Frangula grandiflora* and *F. inconspicua* (cf. discussion for *F. grandiflora* and *F. inconspicua*).

14. Frangula marahuacensis (Steyerm. & Maguire) A. Pool, comb. nov. Basionym: *Rhamnus marahuacensis* Steyerm. & Maguire, Acta Bot. Venez. 14 (3): 22. 1984. TYPE: Venezuela. Amazonas: Depto. Atabapo, Cerro Marahuaca, (Fhuif), cumbre, zona arbolada en la altiplanicie, río arriba, 3°35′ N 65°20′O, 2480–2500 m, 2 Feb. 1982, *J. A. Steyermark, M. Guariglia, N. Holmgren, J. Luteyn & S. Mori 126049* (holotype, VEN not seen, image; isotypes, F not seen, image, NY not seen, image, US not seen, image).

Rhamnus sipapoensis Steyerm., Ann. Missouri Bot. Gard. 75: 1066. 1988, syn. nov. TYPE: Venezuela. Amazonas: Cerro Sipapo (Paráque), rim head of South Basin, occasional in woodland, rugged terrain, 1970 m, 26–28 Jan. 1949, *B. Maguire & L. Politi 28656* (holotype, NY not seen, image; isotypes, COL not

seen, image, K not seen, image, MO, US not seen, image).

In the protologue of *Rhamnus sipapoensis*, Steyermark distinguished his new species from *R. marahuacensis* by its inflorescences being epedunculate to peduncle 6 mm (peduncle 10–25 mm in protologue of *R. marahuacensis*) and by the densely tomentose calyx, pedicels, and stems, "the mainly entire leaf margins; the obtusely acute to abruptly short-acute, mucronate leaf blades" (Steyermark, 1988: 1067) (leaf margins obscurely crenulate and apices rounded-apiculate in protologue of *R. marahuacensis*), and the more densely tomentose abaxial leaf surfaces. Specimens examined found these characters inconsistent, with isotypes of both *R. sipapoensis* (MO) and *R. marahuacensis* (NY) each having some leaves with apices rounded-apiculate and some with apices abruptly short-acute and mucronate. An additional specimen (*O. Huber & L. Izquiero 12825* [MO]) has the rounded-apiculate leaves associated with *R. marahuacensis* and the short peduncle (ca. 2 mm) associated with *R. sipapoensis*. No other differences were found to recognize the two as independent species. Therefore, only *R. marahuacensis* is transferred to *Frangula*, and *R. sipapoensis* is treated as its synonym. Known from the Guayana region of Venezuela, *F. marahuacensis* would be identified, using the key of Johnston and Johnston (1978: 10), as *R. goudotiana*. *Frangula marahuacensis* differs from this taxon most notably in its pubescent ovaries and fruits, often pedunculate inflorescences and infructescences, and the circumscissile hypanthium, contrasting in *F. goudotiana*, its glabrous ovaries and fruits, sessile fascicles of flowers and fruits, and the hypanthium not circumscissile (cf. discussion for *F. chimantensis*).

15. Frangula mcvaughii (L. A. Johnst. & M. C. Johnst.) A. Pool, comb. nov. Basionym: *Rhamnus mcvaughii* L. A. Johnst. & M. C. Johnst., Fl. Neotrop. 20: 50. 1978. TYPE: Mexico. Oaxaca: Sierra de Juárez, Tuxtepec, ca. 50 mi. N of Oaxaca City and 17 mi. S of northernmost high pass, 2800 m, 12 Oct. 1962, *R. McVaugh 21827* (holotype, MICH).

Frangula mcvaughii is similar to *F. pringlei* and *F. wendtii* (Ishiki) A. Pool in having persistent stipules, pedicels long relative to the petioles of the subtending leaves (in *F. mcvaughii*, pedicels 3–5 times the length of the petiole in flower and 4–7 times in fruit) and glabrous ovaries and fruits. It differs from both these species in having leaves with eight to 10 pairs of lateral veins, the lateral veins barely distinguishable from the tertiary veins and initiating at 70–90° angles to the midrib, the ultimate tip of the leaves strongly retuse with the midrib extending as a mucro, and the flowers solitary in the leaf axil versus in *F. pringlei* and *F. wendtii* the leaves with four to seven pairs of lateral veins, the lateral veins easily distinguished from the tertiary veins and initiating at 30–45° angles to the midrib, the ultimate tip of the leaves not retuse, and the flowers in fascicles of one to three (or rarely four) per leaf axil.

16. Frangula neblinensis (Maguire & Steyerm.) A. Pool, comb. nov. Basionym: *Rhamnus neblinensis* Maguire & Steyerm., Mem. New York Bot. Gard. 51: 119. 1989. TYPE: Venezuela. Amazonas: Cerro de la Neblina, summit, near Cumbre Camp, 1800 m, 4 Jan. 1954, *B. Maguire, J. J. Wurdack & G. Bunting 37040* (holotype, NY not seen, image; isotypes, MO, VEN not seen, image).

Rhamnus psilocarpa Maguire & Steyerm., Mem. New York Bot. Gard. 51: 119. 1989, syn. nov. TYPE: Venezuela. Amazonas: Cerro de la Neblina, summit, W escarpment, 1–3 km N of Cumbre Camp, 1700 m, 10 Jan. 1954, *B. Maguire, J. J. Wurdack & G. Bunting 37230* (holotype, NY not seen, image; isotypes, MO, VEN not seen, image).

Rhamnus neblinensis Maguire & Steyerm. and *R. psilocarpa* Maguire & Steyerm. were differentiated (Maguire & Steyermark, 1989; Steyermark & Berry, 2004) by differences in leaf shape and venation; *R. neblinensis* with obovate leaves with rounded apices and cuneate bases and the tertiary venation of the abaxial blade surface elevated and *R. psilocarpa* with oblong or ovate-elliptic leaves with sub-acuminate apices and obtuse bases and the tertiary venation of the abaxial blade surface inconspicuous. However, individual leaves observed on the NY holotype and VEN isotype of *R. psilocarpa* have the leaf shape, apex, and base as described for *R. neblinensis* and some specimens (*M. Nee 30680*, MO, and *N. T. Silva & U. Brazão 60924*, MO) have most of the leaves exhibiting the leaf shape described for *R. psilocarpa* but the conspicuous elevated tertiary venation of *R. neblinensis*. No differences could be found to convincingly differentiate these two names, and *R. psilocarpa* is therefore placed in synonymy under *F. neblinensis*. *Frangula neblinensis* is most similar to *F. acuminata* (cf. discussion for *F. acuminata*).

17. Frangula oreodendron (L. O. Williams) A. Pool, comb. nov. Basionym: *Rhamnus oreodendron* L. O. Williams, Fieldiana, Bot. 29: 547. 1963. TYPE: Costa Rica. San José: along Pan American Hwy. betw. Km. 18 & 20 from El Empalme to Villa Mills, 2700 m, 7 July 1960,

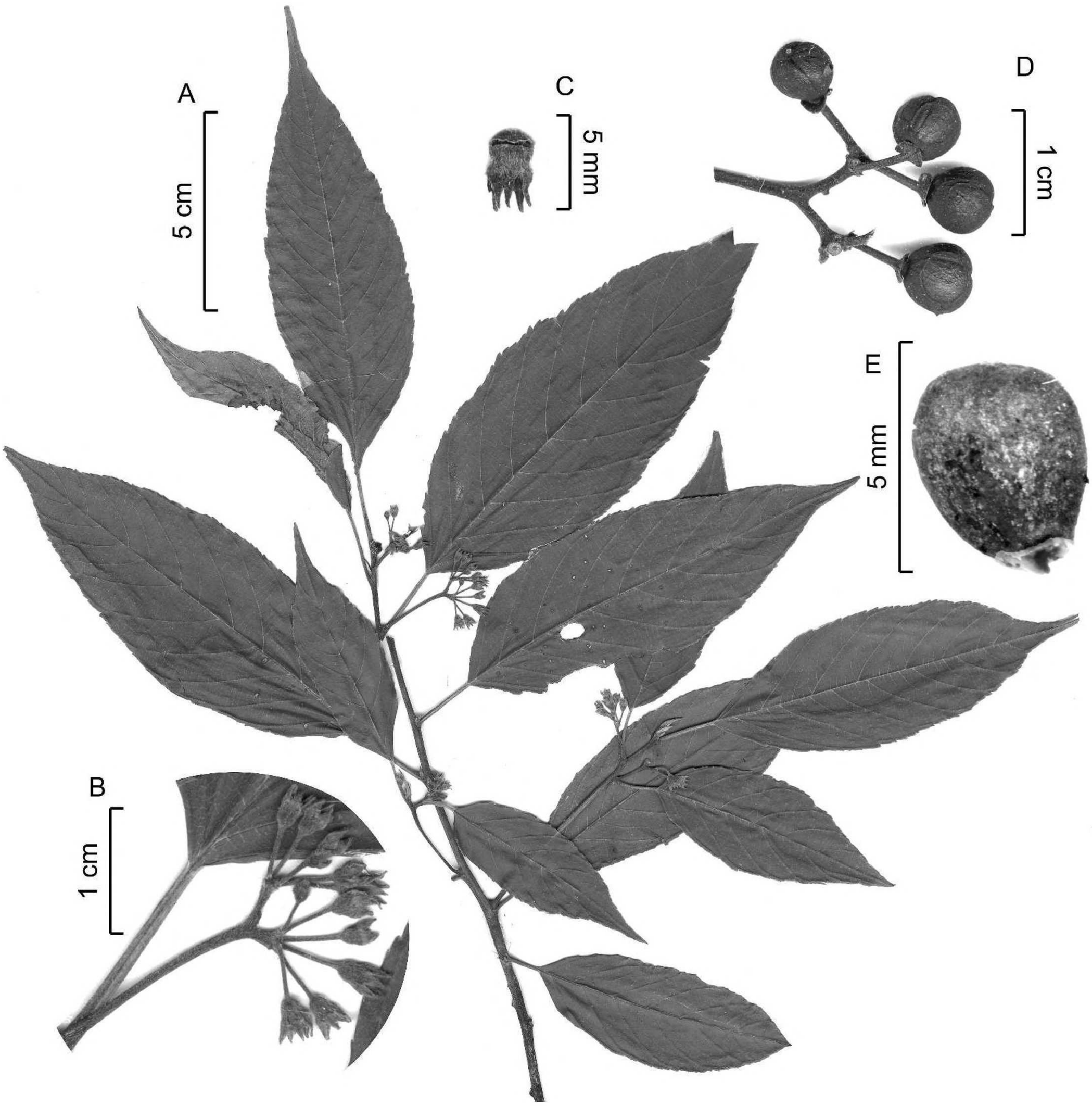

Figure 6. *Frangula pendula* A. Pool. —A. Flowering branch. —B. Inflorescence in leaf axil. —C. Developing fruit with circumscissile hypanthium. —D. Infructescence. —E. Young pyrene with seed exserted at base. A, B taken from the holotype *R. W. Lent 1713* (MO); C from *R. E. Woodson, Jr. & R. W. Schery 492* (GH); D from *W. Haber 644* (MO); E from *J. D. Dwyer 6972* (MO).

M. Cruz 186 (holotype, F; isotype, FLAS not seen).

Frangula oreodendron is one of a few species within the genus distinguished by a non-circumscissile hypanthium (cf. discussion for *F. breedlovei*).

18. Frangula pendula A. Pool, sp. nov. TYPE: Costa Rica. Heredia-Alajuela: Santa Barbara, remnant woods near Quebrada Las Conejas, Concordia, 1800 m, 5 June 1969, *R. W. Lent 1713* (holotype, MO; isotypes, F, NY, US). Figure 6.

Diagnosis. *Frangula pendula* A. Pool is similar to *F. polymorpha* Reissek, differing in the hypanthium tubular, and inflorescences usually strongly divaricate compound cymes and always pedunculate with the pedicels only to 1/3 (rarely to 1/2) the length of the peduncle in flower and to 1/2 the length of the peduncle in fruit.

Small to large trees or shrubs, 2–10 m (occasionally 20–30 m); young branches abundantly to sparsely tomentose or pilose or with appressed and ascending trichomes, trichomes off-white or pale gold. Leaves with blades 6–15 × 2.4–6.3 cm, elliptic, membranaceous, unicolored, with 7 to 12 pairs of lateral veins, lateral veins at 30–60° angles to midrib,

adaxial blade surface with abundant to sparse appressed and ascending trichomes on surface and venation or the indument just on midrib and lateral veins, rarely trichomes tufted in pairs, abaxial blade surface with numerous appressed and ascending to spreading trichomes on all ranks of venation to trichomes sparse on midrib and lateral veins, sometimes trichomes in tufts of 2 or 3, rarely macroscopically conspicuously concentrated along sides of midrib and/or in angles of lateral veins, blade base cuneate or rounded, margin flat or recurved, serrulate, serrate or sometimes only the apical glands apparent, with 3 to 9 teeth/centimeter, apex acuminate or obtuse then cuspidate, sometimes falcate, tip often mucronate; stipules early caducous, 2.5–4 mm; petiole 9–20 mm. Inflorescence a pedunculate and usually divaricate compound cyme, each ultimate group with 2 to 22 flowers, primary peduncles 6–25 mm, (–0.5)0.7–1.7 times length of subtending petiole (length and relative lengths similar in fruit); pedicels 2–5 mm in flower, 1/8–1/3(–1/2) the length of peduncle, 1/8–1/4(–1/2) the length of subtending petiole (2–7 mm long in fruit, 1/7–1/2 the length of peduncle, 1/6–1/3(–1/2) the length of subtending petiole). Flowers 2.75–4(4.5) mm, with the hypanthium tubular, 1.5–2.3 × 1.75–2.8 mm, hypanthium width 1/2–3/4(4/5) of the length of flower with few to numerous, appressed and ascending to spreading trichomes, with circumscissile dehiscence, the sepals, petals, and stamens lost early with upper portion of hypanthium; sepals 1–2.1 × 0.75–1.4 mm, 1/2 to slightly longer than hypanthium in length, erect; petals 0.7–1.2 mm long and wide, broadly or deeply apically bi-lobed, glabrous or with a few trichomes abaxially on midrib, slightly exserted; stamens with filaments 0.5–0.8 mm, anthers 0.4–0.6 mm, infrequently visible free from petals; ovary glabrous, style (0.5)0.9–1.3 mm, stigma 3-lobed. Young fruits 1 to 4 in ultimate groups, glabrous, globose, 3 lines not observable to conspicuous; all sepals, petals, and stamen filaments rapidly lost, hypanthium remnant 0.5–1 × 2–3 mm, not angled; pyrenes 3, ca. 5 × 4.5 mm.

Phenology. *Frangula pendula* was collected in flower between April and July.

Frangula pendula was treated in the *Flora of Panama* (Nowicke, 1971; illustration in Nowicke, 1971: 269, tab. 1) as *Rhamnus pubescens* (Ruiz & Pav.) Triana & Planch. (a later homonym of *R. pubescens* Poir. and treated herein as *F. pubescens*). The latter name, and the species recognized here as *F. pendula*, were both encompassed in Johnston and Johnston (1978) as part of their extremely variable *R. sphaerosperma* var. *pubescens*, which Johnston (1984) referred to *R. sphaerosperma* var. *polymorpha* (cf. discussion for *F. polymorpha*). *Frangula pendula*, with its pedunculate compound inflorescences and glabrous ovaries, is most similar to *F. polymorpha*. *Frangula polymorpha*, endemic to Brazil and Paraguay, differs from *F. pendula* in the hypanthium being funnelform (vs. tubular in *F. pendula*), the petals being strongly exserted with often the whole limb and upper part of the claw exserted and the anthers often free above the petals (vs. only apex of petals exserted and anthers rarely visible above petals), the inflorescences being sometimes sessile, often not compound, divaricate or not (vs. always pedunculate and usually strongly divaricate-compound), and the pedicel in flower 1/3–2 times the peduncle and in fruit 1/2–5 times the peduncle (vs. 1/8–1/3[1/2] in flower and 1/7–1/2 in fruit). Another similar species (and also included in Johnston & Johnston [1978], as *R. sphaerosperma* var. *pubescens*) is the Andean species *F. pubescens*. It differs from *F. pendula* most markedly in its pubescent ovaries and fruits (vs. glabrous in *F. pendula*), subcoriaceous leaves (vs. membranaceous) and variable inflorescences (sessile fascicles, pedunculate simple cymes and compound cymes vs. always pedunculate and usually divaricate compound cymes). Known from Jamaica and Cuba, *F. sphaerosperma* differs from *F. pendula* in its persistent stipules (vs. caducous in *F. pendula*), the hypanthium campanulate (vs. tubular) and flowers 1.75–3 mm long, and approximately equal to the width of the hypanthium (vs. 2.75–4.5 mm and 1.25–2 times the hypanthial width). Occurring in Puerto Rico and Hispaniola, *F. longipedicellata* is similar to *F. pendula* in flower shape and size but always has long pedicels (5.5–9 mm in flower and 8–15 mm in fruit vs. 2–5 mm in flower and 2–7 mm in fruit in *F. pendula*). The pedicels in *F. longipedicellata* are longer than, or rarely in fruit equivalent to, the peduncle length (the peduncle 1–2(4) mm in flower and 1–2(10) mm in fruit, or absent) versus, in *F. pendula*, 1/8–1/2 the peduncle length (the peduncle 6–25 mm).

Distribution. The new species is known from northwestern Costa Rica to northern Panama, where it has been collected commonly between 1100 and 2200 m in montane wet forest. *Frangula pendula* has been rarely collected at lower elevations, between 500 m and 1100 m.

IUCN Red List category. *Frangula pendula* is Data Deficient (DD), according to IUCN (2012) criteria. It is distributed from northwestern Costa Rica to northern Panama. I have seen 75 collections made between 500 and 2200 m in elevation. Its EOO

is ca. 12,600 km² and the AOO is 212 km². Forty-five percent of the known paratype collections were made in protected areas.

Paratypes. COSTA RICA. **Alajuela:** Zarcero, Cerro Palmira, Naranjo, 28 June 1941, *A. Smith 2829* (F). **Cartago:** Empalme, 14 July 1962, *C. A. Brown 17391* (F); Santa María de Dota, 14 July 1962, *C. A. Brown 17390* (F); Carpintera, Hac. Polini, 7 June 1911, *H. Pittier 3667* (F, GH, NY, US); Cartago, Finca Banderilla, San Nicolás, 5 km N del Puente Negro, 9°54′5″N 83°54′41″W, 18 Sep. 1991, *Á. Fernández 142* (CAS, INB not seen, MO); Lankester Gardens, 17 July 1971, *R. W. Lent 2010* (F, MO, NY); Paraiso, Las Concavas, Aug. 1919, *C. H. Lankester K302* (F); Turrialba, terrenos del Instituto, 24 June 1949, *J. León 1651* (US). **Guanacaste:** Liberia, P. N. Rincón de la Vieja, Cordillera de Guanacaste, 10°47′30″N 85°21′15″W, 18 Sep. 1994, *K. Taylor 226* (INB not seen, MO). **Heredia:** rd. N of Gethsemini de Heredia, 19 May 1973, *G. S. Hartshorn 1204* (F, MO), *1205* (F, MO). **Puntarenas:** Cantón de Buenos Aires Sabanas de Murur-Bisuk, cabeceras del Río Ceibo, 9°19′48″N 83°16′48″W, 27 Sep. 1989, *A. Chacón 443* (CR not seen, MO); Parque Nac. Amistad, Las Tablas, near Río Cotón, 8°57′N 82°47′W, 16 July 1982, *C. A. Todzia, L. Diego Gómez P. & R. W. Pohl 1925* (NY, TEX); foothills, Cordillera de Talamanca, valley of Río Cotón betw. Sitio Cotón [Cotonsito] & Sitio Tablas, 8°57′N 82°46′W, 2 Sep. 1983, *G. Davidse 24433* (MO); Fila El Tigre, SE of Las Alturas, 8°56′N 82°51′W, 29 Aug. 1983, *G. Davidse 24180* (MO); 7.5 km NE of Sabalito, 8°51′N 82°53′W, 7 July 1977, *G. L. Webster 21877* (F, TEX); Coto Brus, cuenca Térraba-Sierpe, hac. La Amistad, Zona Protectora Las Tablas, 27 Mar. 2002, *R. Kriebel 6* (MO); Parque Internac. La Amistad, San Vito Coto Brus, Finca Cafrosa, 8°54′00″N 82°46′48″W, 4 July 1990, *R. Delgado 33* (INB not seen, MO); Monteverde, 2 July 1980, *W. A. Haber 389* (MO), 13 Oct. 1984, *W. A. Haber 644* (MO, NY), 9 Sep. 1988, *W. A. Haber 8721* (CR not seen, MO); Buenos Aires, cuenca Térraba-Sierpe, Est. Tres Colinas, Finca Victor Arias, 9°06′40″N 83°04′08″W, 12 Sep. 1996, *E. Alfaro 813* (INB not seen, MO); headwaters of Quebrada Dorora, ca. 9 km NE of Ujarrás, Cordillera de Talamanca, 9°17′24″N 83°15′36″W, 11 Mar. 1993, *M. H. Grayum 10260* (INB not seen, MO); Reserva Indigena Ujarrás, Cordillera de Talamanca, Reserva Biol. Durika, 9°16′30″N 83°14′40″W, 6 Sep. 1995, *R. Aguilar, Q. Jiménez M. & Curso Botánica Amistad 4331* (INB not seen, MO); Coto Brus, Zona Protectora Las Tablas, cuenca Térraba-Sierpe, camino a Las Tablas, 8°55′29″N 82°47′47″W, 28 May 1998, *B. Gamboa R. 2166* (MO); rd. betw. Sitio Tigra & Sitio Las Tablas, near Cerro Chivo, S of Cotón river, 17 July 1983, *D. L. Hazlett 5236* (F); Zona Protectora Las Tablas, Cordillera de Talamanca, Finca Cafrosa, en el tajo, 8°55′15″N 82°47′20″W, 21 June 1996, *E. Navarro V. 365* (INB not seen, MO, NY). **San José:** El Tablago, 8 June 1941, *J. León 818* (F); Zona Protectora Cerros de Escazú, cuenca del río Tarbaca, 9°49′12″N 84°06′00″W, 15 July 1991, *J. F. Morales 37* (MO); Acosta, Fila Bustamante, Cerro Caraigres, 9°43′48″N 84°11′24″W, 22 Apr. 1995, *J. F. Morales & V. Ureña 3998* (CR not seen, MEXU, MO); Alajuelita, near base of Montaña de Cruz SW of Escazú, 9 June 1972, *D. E. Stone 3344* (DUKE not seen, MO); Aserri, alrededores de Barrio Las Mercedes, 9°51′30″N 84°06′00″W, 28 Apr. 1998, *Ó. Valverde 848* (F); Desamparados, vic. of Altos Tablazo ca. 7 km W of Tablón & SE of Higuito, 2 July 1977, *F. Almeda, R. L. Wilbur & T. F. Daniel 2838* (CAS, TEX); Altos Tablazo, ca. 10 km W of Tablón & SE of Higuito, 2 July 1977, *R. L. Wilbur, F. Almeda & T. F. Daniel 21765* (CAS, F, MO, NY); 5 km N de Santa María de Dota, carr. a El Empalme, 9°40′48″N 83°58′12″W, 14 July 1993, *E. Lépiz et al. 35* (CAS, CR not seen, MO); ca. 7.4 km rd. W of Santa María de Dota, 28 Aug. 1968, *R. L. Wilbur & D. E. Stone 10516* (DUKE not seen, MO); Escasú, Cerro de Protti, 31 Aug. 1835, *F. Solís R. 305* (F, MO); Tarrazu, San Marcos, ladera SE del Cerro San Pedro, 9°41′05″N 83°59′48″W, 28 Sep. 2000, *J. Sánchez G., A. Cascante & A. Estrada 999* (CR not seen, F, MO). PANAMA. **Chiriquí:** 13–22 mi. NW of Volcán near Costa Rica border, 13 Sep. 1972, *A. H. Gentry 6026* (MO); Finca en Jaramillo Abajo, 24 Apr. 1986, *A. Taymes s.n.* (MO); Cerro Punta region, Alto los Guerra rd. W of Bambito, 8°53′N 82°37′W, 13 July 1983, *C. W. Hamilton & K. Krager 3889* (MO); Hartman finca, near Cerro Pando, 8°52′N 82°45′W, 22 Aug. 1982, *C. W. Hamilton, H. Stockwell & A. Aiello 807* (MO), *813* (MO); 3 mi. N of El Volcán, 26 June 1969, *E. L. Tyson 5722* (MO), *5725* (MO); Km. 7 on Volcancito rd. W of Boquete, 14 May 1971, *G. R. Proctor 31885* (LL, MO); above Los Llanos, 8°47′N 82°38′W, 3 June 1986, *G. McPherson 9256* (MO); along rd. to top of Volcán Baru, 8°45′N 82°30′W, 28 July 1987, *G. McPherson 11334* (MO); vic. of Volcán Baru, near lake shore at Los Lagos de Volcán, 8°45′N 82°40′W, 9 June 1986, *G. McPherson 9456* (MO); gully 0.5 mi. NE of Volcán, 8°47′N 82°38′W, 14 June 1971, *G. L. Webster & G. J. Breckon 16565* (LL, MO); 3.2 km along side rd., E 7.2 km from Río Sereno off rd. from Volcán to Río Sereno, 29 June 1977, *J. P. Folsom 4031* (MO); near Costa Rican border, 13 km by rd. S of Río Sereno, Finca Hartman, 8°50′N 82°45′W, 12 May 1991, *N. Hensold 1012* (F, MO, TEX, US); vic. Finca Lerida, S slopes of Quebrada Velo, 25 July 1947, *P. H. Allen 4737* (F, MO); Río Chiriquí Viejo valley, near El Volcán, 31 July 1938, *P. White 204* (F, MO); vic. of Finca Lerida, 7–11 July 1940, *R. E. Woodson, Jr. & R. W. Schery 209* (GH, MO, US); vic. of callejón seco, Volcán de Chiriquí, 17 July 1940, *R. E. Woodson, Jr. & R. W. Schery 492* (GH, MO, US); Reserva Forestal de Fortuna, Sendero Samudio, 8°43′40″N 82°15′51″W, 20 June 2004, *R. Aizprúa & I. Alvarez B4234* (F, MO, PMA not seen, SCZ not seen, US); beside Crawford Apis site, El Mirado, Alto Quiel, 5 July 1984, *R. J. Schmalzel 1952* (MO); above Jaramillo, 30 Apr. 1983, *R. J. Schmalzel 1493* (MO); Parque Nac. la Amistad, 7 May 1993, *R. A. Pérez, S. Aguilar, A. Hernández & R. B. Foster 708* (F); Alto Quiel-Boquete a 4 km de finca La Fortuna, 15 Aug. 1977, *T. Béliz 244* (F, MO, NY, US); along rd. betw. Volcán & Río Sereno, 13.7 mi. W of Volcán, 8°51′N 82°43′W, 17 June 1987, *T. B. Croat 66339* (MO); Boquete, carr. hacia Bajo Mono, 3 Oct. 1992, *E. Hidalgo de Montenegro & E. Montenegro 102* (F); E slope of Volcán de Chiriquí (Barú), WNW of Boquete, 19 Nov. 1975, *G. Davidse & W. G. D'Arcy 10157* (MO, NY); rd. from Alto Boquete to Bajo Volcancito, 8°46′N 82°26′W - 8°46′N 82°27′W, 20 June 1971, *G. L. Webster 16656* (LL, MO); Boquete, 5 Sep. 1967, *J. D. Dwyer 6972* (MO); Cerro Horqueta, 8 Aug. 1967, *J. D. Dwyer & M. V. Hayden 7575* (GH, MICH); Boquete, 29 July 1972, *J. Massola 21* (MEXU, MO); Finca Collins, vic. of Boquete, 24 July 1966, *K. E. Blum & J. D. Dwyer 2540a* (GH, MO); Boquete, 27 June 1938, *M. E. Davidson 804* (A, F, MO, US), 26 June 1938, *M. E. Davidson 1066* (F, MO, US); 4 mi. above Boquete on rd. to Volcán Barú, 18 May 1976, *T. B. Croat 34856* (MO), *34859* (MO); above Boquete on rd. to Cerro Horqueta, 12 Aug. 1974, *T. B. Croat 27038* (MO); Renacimiento,

Jurutungo-Piedra Candela, 8°53′N 82°44′W, 28 Sep. 1996, *C. Galdames, J. E. Aranda B., L. Guillén & B. Araúz 3483* (MO).

19. Frangula polymorpha Reissek in Martius, Fl. Bras. 11(1): 91. 1861. *Frangula polymorpha* α [var.] *glabra* Reissek in Martius, Fl. Bras. 11(1): 91. 1861. *Rhamnus sphaerosperma* var. *polymorpha* (Reissek) M. C. Johnst., Taxon 33: 124. 1984. TYPE: Brazil. "In prov. Minarum," *Claussen s.n.* (lectotype, designated here, W not seen; isolectotype, BR not seen, image).

Reissek (1861) published *Frangula polymorpha* with three varieties, α variety *glabra* Reissek, β variety *pubescens* Reissek, and γ variety *tomentosa* Reissek, and 13 syntypes, all of which were associated with one of the above varietal names. There was no indication as to which of the varieties was to be treated as the typical variety. Johnston and Johnston (1978: 67) considered the α variety of Reissek (1861) to be the typical variety, but did not formally recognize it as such. Here, ambiguity is removed by selecting the only syntype associated by Reissek (1861) with the name *F. polymorpha* α [var.] *glabra*, *Claussen s.n.*, as the lectotype of the species, *F. polymorpha*, and thereby establishing *F. polymorpha* α [var.] *glabra* as the typical variety, to be treated under the autonym *F. polymorpha* var. *polymorpha*.

Johnston and Johnston (1978) treated the species *Frangula polymorpha*, with all three of Reissek's varieties referred to a single variety of *Rhamnus sphaerosperma*, which they called *R. sphaerosperma* var. *pubescens* (Reissek) M. C. Johnst. [≡ *F. polymorpha* var. *pubescens* Reissek] (Johnston, 1971). Johnston (1984: 124) nomenclaturally corrected this name to *R. sphaerosperma* var. *polymorpha* (Reissek) M. C. Johnst. to comply with the Demoulin rule that establishes the priority of autonyms over names of the same date and rank (Art. 11.6, McNeill et al., 2012). *Frangula sphaerosperma* (*R. sphaerosperma*, endemic to Jamaica and Cuba) differs from *F. polymorpha* in its flowers with campanulate hypanthia and the width of the hypanthium ca. equal to the length of the flowers versus flowers with funnelform hypanthia and width ca. 2/3 of the length of the flower. *Frangula polymorpha*, as treated here, is known from Brazil (Minas Gerais [e.g., *H. S. Irwin et al. 30310*, MO] and Goiás [e.g., *H. S. Irwin et. al 10729*, MO, US] south to Rio Grande do Sul [e.g., *R. Wasum 350*, MO]) and Paraguay (e.g., *I. Basualdo 1702*, MO). Johnston and Johnston (1978) included 25 names in synonymy below *R. sphaerosperma* var. *pubescens*, which they treated from Costa Rica to Argentina, and in South America including the Andes and the mountains of southeastern Brazil. Please see discussion for *F. pendula* and *F. darienensis* with respect to the Central American species and for *F. pubescens* relative to the Andean species. *Frangula chrysophylla* Reissek from southeastern Brazil is also considered distinct here, differing from *F. polymorpha* (and *F. sphaerosperma*) in its pubescent ovaries and fruits, and the abaxial leaf surfaces are densely covered with appressed stellate trichomes. In both *F. polymorpha* and *F. sphaerosperma*, the ovaries and fruits are glabrous and the leaves are without stellate trichomes. *Frangula chrysophylla* overlaps in geographic distribution with *F. polymorpha* in southeastern Brazil. Other names are not dealt with at this time.

20. Frangula pubescens (Ruiz & Pav.) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 273. 1949. Basionym: *Ceanothus pubescens* Ruiz & Pav., Fl. Peruv. 3: 6, t. 228, f. b. 1802. *Rhamnus pubescens* (Ruiz & Pav.) Triana & Planch., Ann. Sci. Nat., Bot., sér. 5, 16: 379. 1872, non *Rhamnus pubescens* Poir. in Lam., Encycl. 4: 464. 1798. TYPE: Peru. "In Andium nemoribus vs. Chacahuassi tractus," *H. Ruiz s.n.* (holotype, P not seen; isotypes, BR not seen, image, MA not seen, image).

Rhamnus citrifolia Rusby, Bull. New York Bot. Gard. 4: 340. 1907. Syn. nov. *Frangula citrifolia* (Rusby) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 276. 1949. TYPE: Bolivia, s. loc., s.d., *M. Bang 1891* (lectotype, designated here, NY-415036 not seen, image; isolectotypes, BM not seen, image, E not seen, image, F not seen, image, GH not seen, K, not seen, image, M not seen, MICH not seen, image, MO, NY-415037, PH not seen, image, US not seen, image, W not seen, Z not seen).

Only one collection (*Bang 1891*) was cited by Rusby in the protologue of *Rhamnus citrifolia* Rusby. Two specimens of this collection at NY are annotated by Rusby as *R. citrifolia*. The more complete of the two, NY-415036, is selected as the lectotype. Examination of typical material led to the placement of *R. citrifolia* in synonymy of *Frangula pubescens*.

Johnston and Johnston (1978) included both *Frangula pubescens* and *Rhamnus citrifolia* in synonymy of *R. sphaerosperma* var. *pubescens* (Reissek) M. C. Johnst. (treated here as *F. polymorpha*). *Frangula pubescens* from Andean South America differs from *F. polymorpha* in having pubescent ovaries and fruits and flowers with the hypanthia tubular and longer than the sepals versus in *F. polymorpha* (from southeastern Brazil and Paraguay) ovaries and fruits glabrous and flowers with hypanthia funnelform and ca. equal in length to sepals. Probably a number of the other names described from the Andes and included by Johnston and Johnston

(1978) as synonyms of *R. sphaerosperma* var. *pubescens* are actually referable to *F. pubescens*, but more study is needed. *Frangula pubescens* differs from *F. sphaerosperma* in its pubescent ovaries and fruits, caducous stipules, tubular hypanthia, and petals only apically exserted versus glabrous ovaries and fruits, persistent stipules, campanulate hypanthia, and petals well exserted.

21. Frangula riojae (Perkins) Grubov, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 8: 275. 1949, as "rioja." Basionym: *Rhamnus riojae* Perkins, Bot. Jahrb. Syst. 45: 465. 1911. TYPE: Peru. "Loreto" [San Martin?]: Rioja, westlich von Moyobamba, 800–900 m, Savannen Gehölz, Sep. 1904, *A. Weberbauer 4697* (lectotype, designated here, G not seen, photo).

The holotype of *Rhamnus riojae* at B was destroyed, and the isotype at G is here selected as the lectotype.

Johnston and Johnston (1978) treated this taxon as synonymous with *Rhamnus granulosa* (Ruiz & Pav.) Weberb. ex M. C. Johnst. [≡ *Frangula granulosa* (Ruiz & Pav.) Grubov]. Based on the ovary of *F. riojae*, described in the protologue as glabrous, and the tubular and circumscissile hypanthium, depicted in the photo of the lectotype, I suggest that this name be removed from the synonymy of *F. granulosa*, which has a pubescent ovary, and a very broadly campanulate to rotate and non-circumscissile hypanthium. I have not seen actual specimens that correspond with the type and description of *F. riojae*.

22. Frangula scopulorum (M. E. Jones) A. Pool, comb. nov. Basionym: *Rhamnus serrata* var. *scopulorum* M. E. Jones, Contr. W. Bot. 12: 6. 1908. *Rhamnus scopulorum* (M. E. Jones) C. B. Wolf, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 122. 1938. TYPE: Mexico. Chihuahua: near Chuichupa, Sierra Madre Mtns., upper end of Guayanopa Canyon, 5000 ft., 23 Sep. 1903, *M. E. Jones s.n.* (holotype, RSA not seen, image).

Jones (1908) published this taxon as a variety of *Rhamnus serrata* Schult., a member of the genus *Rhamnus*, as recognized here. Wolf (1938) recognized this taxon at the species level in the genus *Rhamnus* subg. *Frangula* (Mill.) Gray. Grubov (1949) kept this name in the genus *Rhamnus*, presumably because he did not see the type which has the pyrenes of the *Frangula* kind, indehiscent with the cartilaginous seed base exserted.

23. Frangula surotatensis (Gentry) A. Pool, comb. nov. Basionym: *Rhamnus surotatensis* Gentry, Brittonia 6: 321. 1948. TYPE: Mexico. Sinaloa: Ocurahui, Sierra Surotato, 1–10 Sep. 1941, *H. S. Gentry 6236* (holotype, MICH not seen, image; isotypes, ASU not seen, GH not seen, MO, NY not seen, image, PH not seen, image).

The type of *Rhamnus surotatensis* Gentry [≡ *Frangula surotatensis* (Gentry) A. Pool] was collected in fruit. It is the only collection of this taxon known from Sinaloa, Mexico, and all of its infructescences are without peduncle. Similar Mexican specimens from Nayarit (in flower, e.g., *F. Flores F. 2106*, MO, and in fruit, e.g., *P. Tenorio L. & G. Flores F. 16341*, MO) and Jalisco (in fruit, e.g., *G. González M. et al. 127*, MO), differ from the type in having pedunculate inflorescences and infructescences, a character that can be variable in other species of *Frangula*, especially when the pedicels are equal to or longer than the peduncles, as is the case in most of these specimens. When specimens with flowers of the non-pedunculate element are known, it may be possible to recognize two separate species. *Frangula surotatensis* in the broad sense (Mexico: Sinaloa, Nayarit, and Jalisco) is most similar to *F. capreifolia* var. *grandifolia* (Mexico: Hidalgo, Veracruz, Puebla, Oaxaca, and Chiapas to Costa Rica). *Frangula surotatensis* differs in having flowers with tubular hypanthia, the hypanthium width to 3/5 of the length of the flower, and the sepals erect. In *F. capreifolia* var. *grandifolia*, the flowers have campanulate hypanthia, the hypanthium width is usually approximately equal to 1.5 times (rarely 2/3) the length of the flower, and the sepals are spreading or recurved.

24. Frangula wendtii (Ishiki) A. Pool, comb. nov. Basionym: *Rhamnus wendtii* Ishiki, Novon 5: 167. 1995. TYPE: Mexico. Oaxaca: Mpio. San Miguel Chimalapa, cima del Cerro Salomón, al NO de la Congregación Benito Juárez, ca. 44 km en línea recta al N de San Pedro Tapanatepec, filo del Cerro con selva baja perennifolia, 16°46′15″N 94°11′45″W, 1830 m, 16 abr. 1986, *M. Ishiki I. 1575* (holotype, MEXU not seen; isotypes, CHAPA not seen, TEX not seen, image).

With its persistent stipules, and the pedicels long relative to the petioles of the subtending leaves (pedicels 1.5–3.5 times length of petiole in flower, 2.5–5 times in fruit), as well as the glabrous ovaries and fruits, this species is most similar to *Frangula mcvaughii* and *F. pringlei*. From *F. mcvaughii*, *F. wendtii* differs most markedly in its leaf apex (acuminate vs. obtuse, truncate or acute in *F.*

mcvaughii) and the lateral veins (four to six pairs at 30–45° angles vs. eight to 10 pairs at 70–90° angles). The pedicels in *F. wendtii* are shorter relative to the petioles than in *F. mcvaughii*; in *F. mcvaughii* the pedicels are three to five times the length of the subtending petiole in flower and four to seven times in fruit. From *F. pringlei*, *F. wendtii* differs in leaf shape as elliptic, with acuminate apex, the blade is glabrescent, with the trichomes restricted to the midrib or to the midrib and lateral veins, and the marginal tooth glands not on stalks. In *F. pringlei*, the leaves are usually obovate, sometimes elliptic, with obtuse to rounded to less frequently acute apices, the blade surfaces are pubescent, usually densely so, and the marginal tooth glands are on filiform stalks. The shape of immature fruit is more or less obovate in *F. wendtii* versus obcordate in *F. pringlei*.

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